

ENERGETICS OF NORTHERN PHOCID SEALS: THE INFLUENCE OF SEASONALITY
ON FOOD INTAKE AND ENERGY EXPENDITURE

By

HUGO OCHOA-ACUÑA

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Hugo Ochoa-Acuña

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As in many other mammals, rates of food intake of phocid seals (Family Phocidae) vary throughout the year. Information on seasonal variability of feeding rates and energetics of northern phocid seals is important because of the controversy surrounding metabolic rates of marine mammals and because effective fisheries management requires models of fish consumption by seal populations that explicitly include temporal variation. I studied energetics over in three phocids, the harp (*Pagophilus groenlandicus*), harbor (*Phoca vitulina*), and ringed (*P. hispida*) seals. I analyzed records of food intake and body mass of captive seals. I determined weekly body mass changes, food intake, and activity levels for seven harp, six harbor, and two ringed seals. In addition, I measured basal metabolic rates of five harp, three harbor, and one ringed seals through open-flow respirometry. Oxygen consumption was measured from post-absorptive animals at

different ambient temperatures for periods of 2-4 hours. Some determinations were made throughout the year, but most (10-18 per month) were made in October, January, April, and July on three male harp seals, to determine seasonal changes in basal rates of metabolism. I also established the body composition of four adult harp seals during the four seasons of the year, to determine changes in the energetic equivalency of changes in body mass. Activity levels were monitored using modified Mk6 time-depth recorders, to establish if activity was an important component of the energy budget.

Captive seals undergo profound changes in body mass and food consumption throughout the year, and after accounting for changes in body mass, feeding rates still differ across seasons, which suggests shifts in energy expenditure. The species studied have basal rates of metabolism higher than expected from body mass, but that did not differ from those of terrestrial flesh-eating eutherians. I also determined that shifts in basal rates of metabolism were directly correlated with the observed fluctuations in energy expenditure and food consumption. I also found that changes in body mass of harp seals throughout the year were due not only to changes in the size of body fat stores, but also to changes in lean body mass. The results indicate that changes on basal metabolic rates explain a significant portion of the seasonal variation in energy expenditure, and that these changes may translate into large changes in the amount of fish consumed by the northwest Atlantic harp seal herd.

CHAPTER 1 INTRODUCTION

Natural History of Pinnipeds

Systematics

Pinnipeds (Order Carnivora, families Otariidae, Odobenidae, and Phocidae) are mammals adapted for living both on land and at sea. All species give birth over land or ice (King 1983). In addition, with the exception of the walrus (*Odobenus rosmarus*), lactation occurs almost entirely over solid substrate (Oftedal et al. 1987a).

Until recently there was much debate about whether or not pinnipeds are polyphyletic. Today, based on morphological and biochemical data, it is accepted that both groups (phocids on one hand, and otariids and odobenids on the other) descend from a common ancestor (Sarich 1969, Arnason and Widegren 1986, Wyss 1988).

There are 33 species of extant pinnipeds grouped in three recognized families: Odobenidae, consisting solely of the walrus; Otariidae, consisting of the "eared" seals (fur seals and sea lions); and Phocidae, or "true" seals. The eighteen recognized species of phocids are in turn classified into two subfamilies:

Monachinae (Antarctic phocids plus elephant and monk seals), and Phocinae (northern phocids) (King 1983).

General Biology

Seals are important top predators in many marine ecosystems, and they are especially abundant in highly productive areas, such as polar regions and zones of upwelling. Although most seals feed preferably on nektonic prey such as fish, squid, and krill, bearded seals (*Erignathus barbatus*) and the walrus feed primarily on benthic invertebrates (Bonner 1994).

The young of pinnipeds are born after a 8-10 month gestation period, and offspring are highly precocial at birth. Female pinnipeds give birth to a single pup, and reproduction tends to be highly synchronized, with mating occurring only a few days after parturition. In otariid species, which always breed on land, females nurse their young from four to 24 months, whereas in the mostly ice-breeding phocid species, females suckle their young for only a few weeks or even days (Oftedal et al. 1987a).

Most phocid mothers stay onshore continuously suckling the pup until weaning (but see Boness et al. 1994). During lactation, the mother does not feed and milk production is sustained entirely from body reserves stored before parturition. On the other hand, otariid mothers alternate periods of suckling on land with periods of foraging at sea throughout the more prolonged lactation (Costa 1991).

Ringed, Harp, and Harbor Seals

Ringed seals (*Phoca hispida*) and harp seals (*Pagophilus groenlandicus*) are the most abundant of the northern seals (around 6,000,000 and 4,000,000 individuals, respectively) (Riedman 1990). Although harbor seals (*Phoca vitulina*) are one of the most widespread species of pinnipeds, they are not as abundant (~400,000).

Harp seals occur in Arctic and subarctic waters of the North Atlantic Ocean from around 90° E to 90° W (Ronald and Healey 1981). Harp seals migrate north in the summer and south in winter and spring to breed (Figure 1.1). Harp seals congregate to reproduce on pack ice, where they form huge concentrations. Harp seal pups are born from late February to early March, and are weaned after a 12-day lactation (Bowen and Sergeant 1983). After breeding, adults molt in April-May and then migrate North.

Ringed seals have a wide distribution in seasonally and permanently ice-covered waters of the Northern Hemisphere. They occur through the Arctic basin, and seasonally into the North Atlantic, Hudson and James Bays, and the Chukchi and Bering Seas. Ringed seals are non-migratory and use fast-ice for breeding (Frost and Lowry 1981).

Harbor seals inhabit temperate and subarctic waters of the North Atlantic and North Pacific. On the northwest Atlantic, they can be found from Massachusetts to Hudson Bay. Throughout the

year, harbor seals are littoral in distribution and nonmigratory (Bigg 1981).

Metabolic Rates of Pinnipeds

Some phocid and a few otariid species have been studied through the development of energy budgets to determine the effect of these populations on commercially important fish species (Lavigne et al. 1982, Beddington and de la Mare 1985, Lavigne et al. 1985, Swartzman and Haar 1985, Øritsland and Markussen 1990). A major drawback in estimating food intake of pinnipeds is the paucity and uneven quality of data on metabolic rates and energy expenditure.

Energy Budgets of Pinnipeds

The energetic content of food ingested by an homeotherm must be equal to the sum of energy lost through feces and urine, plus the sum of energy spent as the specific dynamic action of food, and the energy used in the various tasks performed (Lavigne et al. 1982). The following equations summarize how energy is partitioned in a homeotherm:

$$GE = F + U + ME$$

$$ME = SDA + NE$$

$$NE = BMR + TR + A + G + R$$

Where GE = energy content of food; F = fecal losses; U = urinary losses; ME = metabolizable energy; SDA = specific dynamic action of food; NE = net energy; BMR = basal rate of metabolism;

TR = temperature regulation; A = activity; G = growth; R = reproduction.

Fecal and urinary energy losses in pinnipeds have been measured only on grey and harp seals. When fed Atlantic herring (*Clupea harengus*) juveniles from both species lost between 5 - 7.5% of their gross energy intake through feces and 6.9 - 9.9% of their metabolizable energy intake through urine (Keiver et al. 1984, Ronald et al. 1984). Fecal and urinary losses of harp seals were not affected by feeding frequency. However, seals feeding on herring with low energy content had a greater proportion of the energy ingested lost through the feces than seals feeding on herring with high energy content, and this was probably due to the greater nitrogen content of herring with low energy content.

The increase in metabolic rate caused by the digestion and assimilation of food is the specific dynamic action (SDA). The magnitude and duration of the influence of SDA on metabolic rate has been measured in only one pinniped, the harp seal (Gallivan and Ronald 1981). The apparent SDA represented around 17% of the gross energy of the diet, increasing the daily metabolic rate between 11 - 21%, depending on the size of the meal. These authors found that, on a herring diet, metabolic rates did not return to pre-prandial levels until after 10-12 hours.

Basal rates of metabolism are standardized measures used for intra- and inter-specific comparisons. Basal metabolism is the rate of energy expenditure of mature animals at rest, under

thermoneutral conditions, and in a post-absorptive state. The scarcity of data on pinniped and cetacean basal rates of metabolism have fueled a long-standing debate on whether basal rates of marine mammals are comparable to those predicted by the empirical equation relating basal rates of metabolism and body mass developed by Kleiber (1961) using data from domesticated mammals. Historically, it was widely accepted that marine mammals had basal rates higher than those of terrestrial mammals. This assumption was supported with empirical data (Irving et al. 1935, Scholander 1940, Irving and Hart 1957, Hart and Irving 1959, Kooyman et al. 1973, Miller and Irving 1975, Miller et al. 1976), and explained as an adaptation for living in cold water (Irving 1969). On the other hand, some researchers have postulated that pinnipeds do not have higher rates of metabolism when conditions to determine the basal rates are met (Lavigne et al. 1982, Schmitz and Lavigne 1984, Lavigne et al. 1986).

Pinnipeds live in many different climates, from the Arctic and Antarctic to the shores of Australia, and the Hawaiian and the Galapagos Islands. Temperature regulation is accomplished through different adaptations in the different pinniped groups. Fur seals (Genus *Arctocephalus* and *Callorhinus*, family Otariidae) are able to maintain a temperature gradient of 25°C across some 20 mm of fur (Irving et al. 1962). On the other hand, phocid seals, sea lions, and the walrus, have a sparse underfur with relatively little insulative value. These animals have a blubber layer that has multiple functions: serves as energy reserve, adjusts

buoyancy, streamlines the body, and acts as thermal insulation (King 1983, Riedman 1990). Studies on ringed seals have shown that the blubber layer is distributed in such a way that the ratio of blubber thickness to body radius is nearly constant over the body, giving maximal insulation with a given amount of blubber. This agrees with the heat exchange model of a cylinder, in which heat loss does not depend on the wall thickness per se, but on the ratio between wall thickness and the radius of the cylinder (Ryg et al. 1988). Phocid seals use their fat reserves without compromising their thermal insulation. Using computed tomography, Nordoy and Blix (1985) demonstrated that, although the blubber layer provided 94% of the energy used by grey seal (*Halichoerus grypus*) pups fasting for 31 days, the subcutaneous blubber contributed a constant proportional area of the total cross-sectional area of the body. During fasting, harp seals not only lose blubber, but also core mass, thus probably maintaining the ratio between blubber thickness and body radius (Worthy and Lavigne 1987). Northern elephant seal (*Mirounga angustirostris*) pups fasting after weaning also lose body mass, keeping body composition relatively constant (Rea and Costa 1992).

The cost of swimming has been measured in several pinniped species. Pinnipeds exhibit a curvilinear rise in metabolic rate with increasing swimming speed. This is primarily due to the increase in drag. Despite the effect of drag, pinnipeds use less energy for locomotion than terrestrial mammals of similar size, due in part to the absence of postural costs (Feldkamp 1987).

Although phocids and otariids use different means of propulsion (using their rear flippers and fore flippers, respectively), both groups have equivalent minimal costs of locomotion. Adult California sea lions (*Zalophus californianus*) and harbor seals have minimum costs of swimming of 2.5 and 2.3 J / kg m, respectively. These values represent 2.3 and 2.1 times the metabolic rate measured when resting, respectively (Davis et al. 1985, Feldkamp 1987). During diving, Weddell seals (*Leptonychotes weddelli*) have been shown to maintain an almost constant swimming velocity of about 2.0 - 2.1 m/s. These animals did not increase metabolic rate when diving as compared to resting rates (Castellini et al. 1992). However, these results are complicated by possible physiological compensations that occur during diving. The same study found that metabolic rates decreased with an increase in diving duration.

Growth energetics have been studied extensively in pinnipeds. Whereas in otariids lactation lasts more than four months, in phocids the nursing period only lasts from four days to eight weeks. As in terrestrial mammals, resting metabolic rates of growing pinnipeds are higher than those measured in adult animals (Miller and Irving 1975, Lavigne et al. 1986, Markussen et al. 1990). Phocid seal pups are able to efficiently deposit large amounts of blubber in very short periods. Northern elephant seal pups gained 54.9 % of the mass lost by their mothers (Costa et al. 1986).

The energy spent in reproduction has been measured in pinnipeds taking advantage of the temporal separation between foraging at sea and reproductive activity on land. In phocids, females fast during the reproductive period and thus neonatal body mass and maternal mass loss during lactation are good indicators of maternal expenditure (Fedak and Anderson 1982). Males of polygynous species have high levels of expenditure. Southern elephant seal (*Mirounga leonina*) bulls lost body mass at a rate of up to 20 kg per day during their 58-day stay on land, totaling almost 40% of their original mass (Fedak et al. 1994).

The Influence of Body Size and Composition on Metabolic Rates of Phocid Seals

The most important factor influencing metabolic rate among and within species is body mass. Body mass has been shown to explain a large portion of the variation in basal metabolic rates among mammals and birds. In adult animals, changes in body mass are, for the most part, changes in the size of fat stores. Lean body mass is relatively constant not only in size, but also in composition.

There is considerable controversy regarding the relative contribution of adipose tissue to basal rates of metabolism. Many researchers (e.g., Blaxter 1989, Lavigne et al. 1986) have proposed that the contribution of adipose tissue to metabolic rate is insignificant, and that, as a consequence, lean body mass instead of body mass should be used in allometric equations

relating metabolic rate and the size of the animal. However, some studies have demonstrated that adipose tissue is highly active and contributes significantly to the overall heat production (McCracken and McNiven 1983, McNiven 1984).

Parallel to the annual reproductive and behavioral cycle, phocid seals experience large seasonal fluctuations in some physiological characteristics, such as body mass and metabolic rate. Over a four-year period, body mass of some captive adult male harp seals increased from September to May and then decreased from April to August. These fluctuations comprised up to one third of the peak mass (Miller, personal communication). Annual fluctuations in body mass are caused by changes in the thickness of the blubber layer. Here, Renouf and Noseworthy (1991) found an inverse relationship between water temperature and blubber content in harbor seals. Unfortunately, data on seasonal variation on phocid seals is inconclusive. Renouf and Gales (1994) reported a slight or no increase in body mass of harp seals from May to February. Nevertheless, these authors reported mass-specific basal rates of metabolism twice as high in April-July as compared with values from August-March.

Objectives of the Present Study

The apparent conflict between commercial fisheries and pinniped populations make it imperative to develop accurate energy expenditure models for seal species to predict fish consumption. The large sizes of the populations of ringed, harp, and to a much

lesser extent, harbor seals makes the development of precise energy budgets of critical importance. A 500-g difference in the estimated average daily consumption of fish by harp seals translates to a difference of 730,000 metric tons eaten annually by this population. This difference might substantially affect the prediction of the impact of seals on the recovery of Atlantic cod (*Gadus morhua*), given that the spawning stock is estimated to be down to 30 to 50,000 metric tons (Lavigne, personal communication). Although many studies have addressed the question of whether seals prey on commercially important species, few studies have determined basal rates of metabolism, the cost of thermoregulation both in air and in water, and the influence of body fat changes on those parameters. Given that food intake, activity, and body composition of pinnipeds change seasonally, it is necessary to study metabolic rates throughout the year, to construct meaningful predictors of fish consumption.

The purpose of this study was to obtain this information for phocid seals. Research was conducted at the Ocean Sciences Centre of Memorial University of Newfoundland, using the seals, installations, and equipment there available. Chapter 2 addresses the question of the presence and extent of annual cycles of body mass, food intake, and energy expenditure in harp, harbor, and ringed seals. Chapter 3 presents the results of the study of resting metabolic rates in relation to ambient temperature and age, and the estimation of basal rates of metabolism for the three species of phocids mentioned above. Metabolic rates of thirteen

seals (nine harp seals, three harbor seals and one ringed seal) were measured in terms of oxygen consumption in air and in water. Chapter 4 describes the analysis of seasonal changes in energy expenditure and basal rates of metabolism of three adult male harp seals. Chapter 5 analyzes the influence of body composition on energy expenditure and basal rates of metabolism of adult harp seals. Chapter 6 presents the results of the study of activity levels and the cost of activity of captive harp seals. Chapter 7 summarizes the most relevant findings of this study.

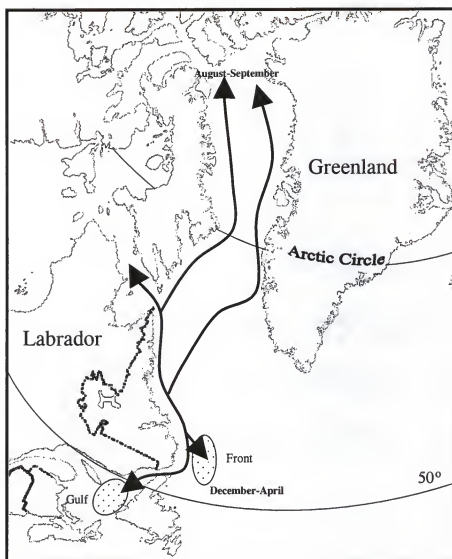


Figure 1.1. Breeding grounds ("Gulf" and "Front", dotted areas), and approximate migration routes of northwest Atlantic harp seals (*Pagophilus groenlandicus*). Approximate dates in which seals stay in the two extreme locations are also provided.

CHAPTER 2
SEASONAL CHANGES IN BODY MASS AND FEEDING RATES OF NORTHERN
PHOCID SEALS

Introduction

Northern phocids live in a highly seasonal environment and, consequently, some aspects of their life history demonstrate a high level of circannual periodicity. For example, female harp seals give birth every year between late February and early March, and nurse their pups for 10-13 days (Sergeant 1991). During lactation, phocid females do not forage, although there is some evidence that harbor seal females perform foraging trips similar to those of otariid seals (Boness et al. 1994). Although most phocid males do not defend territories on solid substrate, as do otariids and phocids belonging to the genera *Mirounga* and *Hydrurga* (elephant and grey seals), they seem to guard females from other males (Riedman 1990), and as a consequence, they might drastically decrease food intake during the breeding season.

The objectives were to determine the presence and extent of seasonal changes in body mass and food intake in three species of northern phocids. The appropriate data were collected from 1987 to 1997, although the length of the records varied from animal to animal.

Material and Methods

This study was conducted at the seal facility of the Ocean Sciences Centre, Memorial University of Newfoundland, in Logy Bay, Newfoundland (47°38'N, 52°40'W). Animals were kept outdoors in a facility consisting of two 12-m-diameter tanks (300-m³ capacity each) and 190 m² of haul-out decking surrounding the tanks. All tanks were cleaned weekly and refilled with seawater pumped from the bay.

Seals were fed daily around 1200 h. Each animal was allowed to eat as much as it wanted for a period of two hours. Food consisted of thawed frozen herring supplemented with vitamins.

I analyzed body mass and food intake records of seven seals held at the Ocean Science Centre, Logy Bay, Newfoundland, to explore the influence of seasonality on body mass and food intake of adult (> 4.0 year-old) harp seals.

Statistical Analyses

Statistical analyses were performed using different statistical procedures from the STAT and ETS modules of the SAS statistical package (SAS Institute Inc. 1985). All values provided are mean $\pm$ standard error, SE.

Body mass and food intake annual cycles

I tested for the presence of annual cycles of body mass and food intake through time-series regression analysis (PROC AUTOREG) using daylength as the independent variable. This procedure

produced parameter estimates corrected for the autocorrelation introduced in the data by sequential sampling of body mass, food intake, and daylength. Data were previously detrended to remove ontogenetic changes in body mass and food intake. In addition, I confirmed the presence of circannual and infrannual cycles of body mass and food intake using spectral analysis (PROC SPECTRA). This procedure uses the finite Fourier transform to decompose data series into a sum of sine and cosine waves, and produce a periodogram which reflects the contribution of each harmonic to the total sum of squares (SAS Institute Inc. 1993).

Changes in maintenance energy requirements

I calculated daily mass change (DMC, g/d) as the difference between two consecutive weighings, divided by the days elapsed between them. Total food intake during these days was averaged and multiplied by the energetic content of the herring fed to the animals (Table 2.1), and by its digestive efficiency (Lawson et al. 1997) to estimate digestible energy intake, DEI. I included only those days in which the sole food type offered was herring, and the seals were completely satiated after the two-hour feeding period.

Energy intake at constant body mass (maintenance energy intake, MEI) was calculated through regression analysis (x intercept of DMC regressed against DEI) for each of the different periods (i.e., seasons) in which each year was divided (Table 2.2). In addition, I calculated the mean of body mass, DMC, and DEI for each of these periods.

Relationship between body mass and food requirements

I tested the null hypothesis that MEI of adult seals was not related to body mass. I regressed mass-specific MEI against body mass of adult (> 4 years old) seals. I included 'seal' as a factor in the linear model to account for possible individual differences.

Results

Body mass of adult harp seals (> 4.0 years old) varied from a minimum during summer to a maximum during spring, with an average value of 146.7 ± 25.9 kg (Table 2.3, Figures 2.1-2.5). Adult harbor seals had a mean body mass of 87.2 ± 4.9 kg that varied from a minimum in the fall to a maximum in summer (Table 2.3, Figures 2.6-2.8). Body mass of the two ringed seal studied varied from a minimum during the summer to a maximum in winter, with a mean of 45 ± 2.8 kg (Table 2.3, Figure 2.9).

Seasonal Differences

Harp seals

Although 63.7% of the variation in body mass was due to inter-individual variation, and only 10.2% was due to seasonal effects, these were highly significant ($F_{3,90}=13.6$, $P<0.0001$) (Figure 2.10). Individual differences in the rate of daily mass change were not significant ($F_{7,89} = 0.7$, $P=0.7$), and season explained most (31.2%) of its variation ($F_{3,89}=14.3$, $P<0.0001$).

Body mass did not have an effect on the rate of mass change ($F_{1,90}=3.2$, $P=0.08$).

Food intake varied from a minimum during the fall to a maximum in winter, with a mean of 32.2 ± 3.06 MJ/d (Figure 2.11). Individual seals had similar levels of food intake, and season was the only significant factor in the model, explaining 29% of the total variation ($F_{3,89}=15.0$, $P<0.0001$).

The analysis of the relationship between daily mass change and energy intake revealed that harp seals in captivity changed their level of energy expenditure throughout the year. Maintenance energy requirements were lowest during fall and highest during spring, with a mean value of 31.3 ± 2.96 MJ/d (Figure 2.12). Individual seals had similar maintenance requirements, and 20.4% of the overall variation was due to seasonality ($F_{3,47}=5.3$, $P<0.0031$). Body mass had no effect on maintenance requirements ($F_{1,47}=0.1$, $P=0.81$).

Harbor seals

Body mass of harbor seals varied from a maximum in summer to a minimum during the fall (Figure 2.10). The influence of season on body mass of harbor seals was highly significant ($F_{3,113}=11.3$, $P<0.0001$) explaining 18.5% of the total variation. Individual differences were also significant ($F_{5,113}=7.7$, $P<0.0001$) and accounted for 20.9% of the total variation in body mass. Season also had an effect on the rate of daily mass change ($F_{3,112}=11.9$, $P<0.0001$) accounting for 23.3% of the total variation, whereas

individual differences and body mass effects were not significant ($F_{3,112}=0.67$, $P=0.6274$; $F_{1,112}=2.1$, $P=0.1498$, respectively).

Food intake of harbor seals was maximal during the fall, declining thereafter until summer (Figure 2.11). Season explained 20.6% of the total variation in the rate of feeding ($F_{3,112}=11.7$, $P<0.0001$), and individual differences explained 8.6% ($F_{3,112}=2.9$, $P<0.02$). Body mass had no influence on feeding rates ($F_{1,112}=7.7$, $P<0.0001$).

I found that harbor seals displayed seasonal changes in their level of energy expenditure (Figure 2.12). Season explained 10.6% of the total variation in maintenance requirements ($F_{3,46}=3.3$, $P<0.03$). Individual differences accounted for 23.7% of the total variation ($F_{3,46}=4.4$, $P<0.003$) whereas body mass effects were not significant ($F_{1,46}=1.8$, $P=0.1831$).

Ringed seals

The two ringed seals studied did not display seasonal changes in body mass ($F_{3,13}=1.0$, $P=0.4433$) (Figure 2.10). Individual differences were also not significant ($F_{1,13}=2.2$, $P=0.1581$). The rate of daily mass change was not influenced by individual differences ($F_{1,12}=4.1$, $P=0.0649$), season ($F_{3,12}=1.6$, $P=0.2492$), or body mass ($F_{1,13}=1.1$, $P=0.3242$).

Ringed seals had maximal levels of food intake during spring and minimal during summer (Figure 2.11). Season explained 45.6% of the total variation in food intake ($F_{3,12}=4.7$, $P<0.03$). Individual differences explained 18.5% of the variation in feeding

rates ($F_{1,12}=5.8$, $P<0.035$) and body mass explained 22.5% ($F_{1,12}=7.0$, $P<0.03$).

I found that energy expenditure of ringed seals was not influenced by season ($F_{3,3}=0.7$, $P=0.5996$), individual differences ($F_{1,3}=0.6$, $P=0.4794$), or body mass ($F_{1,3}=2.0$, $P=0.2535$) (Figure 2.12).

Influence of Photoperiod

All the harp seals that were two years old or older and for whom at least one year of data was available showed an inverse relationship between daylength and body mass (Table 2.4). Food intake also increased with decreasing photoperiod during spring and fall (Figure 2.13). Conversely, only the female harbor seal (KEV) demonstrated a relationship between photoperiod and body mass, but food intake was strongly influenced by photoperiod (Figure 2.14). The two ringed seals included in this study also showed an inverse relationship between photoperiod and body mass, although no clear pattern was observed between daylength and food intake (Figure 2.15).

Discussion

This study demonstrated that harp, harbor, and ringed seals displayed profound seasonal changes in food intake. Levels of energy expenditure of harp and harbor seals were also influenced by seasonality. I did not detect seasonal effects on body mass and energy expenditure of ringed seals, and this was probably related to the small sample size ($n = 2$).

Seasonal changes in body mass have been reported for a number of pinniped species (Boulva and McLaren 1979, Ashwell Erickson and Elsner 1981, Fedak and Anderson 1982, Stewart and Lavigne 1984, Costa *et al.* 1986, Bowen *et al.* 1987). The cycles of body mass have been related to reproduction, with pronounced mass loss occurring during lactation and rutting, and the annual moult (Ryg *et al.* 1990). Changes in body mass do not seem to be only a consequence of food availability. This and other studies performed under *ad libitum* conditions demonstrate that pinnipeds vary food intake throughout the year, and that the resulting body mass cycles closely resemble those observed in the wild (Ryg *et al.* 1990, Renouf and Noseworthy 1990, Kastelein *et al.* 1990a,b,c,1991,1995). Lager *et al.* 1994 found that harp seals kept at the natural photoperiod observed at 69°N also increased mass from fall to spring, and that food intake reached a maximum during winter. These data suggest that the observed variation in body mass of wild seals cannot be attributed directly to variations in food availability.

The spatial separation between feeding and breeding grounds, and the high degree of synchrony of the breeding events may have favored the development of internal circannual rhythms of food intake among phocids. Animals tend to have lower levels of energy expenditure when food consumption is low or null (e.g., Grande *et al.* 1958, Felig *et al.* 1983, Elliot *et al.* 1989). This metabolic depression may be explained by the recession of organs involved with food processing that have a high metabolic intensity (Burrin

et al. 1988, Daan et al. 1989, Burrin et al. 1990, Konarzewski and Diamond 1995). Thus, phocids may concentrate feeding during only some periods of the year, and withdraw from food consumption when food availability is low.

Another factor that may contribute to the development of annual cycles of food consumption in phocids in particular, and mammals in general, is the necessity to devote significant amounts of time to search for mates, defend territories, chase competitors, and nurse pups during the seasonal and synchronized breeding events. Renouf et al. (1988) observed a negative correlation between the number of social interactions and the rate of food intake in a group of captive harbor seals. Korhonen and Harri (1986) found that food intake and activity of farmed polecats (*Mustela putorius*) varied inversely during the year.

My observations of cyclic anorexia in northern phocids suggest that they rely on environmental cues, other than food availability, to regulate food intake. Harp seals decreased food intake with increasing photoperiod, both during spring and summer (Figure 2.13). Harbor seals decreased food intake with increasing photoperiod throughout the entire range of daylengths (Figure 2.14). No clear trend between photoperiod and food intake was observed for the two ringed seals (Figure 2.15). Harp seals in the wild experience a different pattern of change of daylength throughout the year, because of their annual migration. However, the photoperiods experienced by the seals studied, and those experienced by wild seals were not different during the periods of

the year in which photoperiod had an effect on food intake (spring and summer) (Figure 2.16).

No previous study has addressed the possible changes in the level of energy expenditure throughout the year in northern seals. My study demonstrated that almost 40% of the variability in energy expenditure was related to seasonal effects. Given that a major component of the energy expenditure of homeotherms is the basal rate of metabolism, these results point to the possibility that basal metabolism changes throughout the year in these species.

Table 2.1. Proximate composition of herring, *Clupea harengus*, fed to seals kept at the Ocean Sciences Centre, Logy Bay, Newfoundland (fresh weight basis).

Fed-from	Fed-to	N	Protein, %		Lipid, %		Energy, kJ/g	
			$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
20-Apr-91	08-Aug-91	5	17.3	0.84	11.3	0.50	8.4	0.39
09-Aug-91	18-Nov-91	5	18.8	0.93	7.6	0.31	7.3	0.06
19-Nov-91	31-Mar-92	5	16.7	0.80	13.9	0.64	9.2	0.59
01-Apr-92	01-May-92	5	17.4	0.84	9.9	0.43	7.8	0.47
02-May-92	08-May-92	5	17.4	0.84	6.3	0.25	6.5	1.03
09-May-92	21-May-92	5	17.3	0.83	6.4	0.26	6.4	0.72
22-May-92	04-Aug-92	5	15.5	0.73	15.4	0.72	9.6	0.71
05-Aug-92	10-Aug-92	5	16.1	0.77	9.3	0.40	7.3	0.32
01-Jan-93	01-Nov-93	10	21.0	0.47	10.0	0.76	9.8	0.23
02-Nov-93	05-Nov-93	4	19.5	0.29	16.1	1.60	10.7	0.56
06-Nov-93	04-Jun-94	7	19.5	0.25	16.7	0.48	11.0	0.15
04-Jun-94	16-Jun-94	5	19.8	0.50	11.2	3.18	8.9	1.13
09-Dec-94	13-May-95	3	17.1	0.60	12.3	0.37	8.7	0.28
14-May-95	25-Aug-95	6	18.7	0.56	8.7	0.98	7.7	0.33
16-Oct-95	09-May-96	3	18.7	0.67	11.8	1.29	8.9	0.59
02-Oct-96	31-Oct-96	2	18.1	0.31	6.2	0.23	6.6	0.02
01-Nov-96	20-Aug-97	10	19.1	0.47	8.4	0.67	7.7	0.28

Table 2.2. Periods (seasons) among which years were divided in relation to daylength observed in Logy Bay, Newfoundland (47°38'N, 52°40'W).

	Start	End	Period length (days)	Minimum day length (h)	Maximum day length (h)	Change in daylength (min/d)
Decreasing days (Fall)	Aug 6	Nov 4	91	9.9	14.7	3.3
Short days (Winter)	Nov 5	Feb 6	94	8.4	9.8	1.8
Increasing days (Spring)	Feb 7	May 6	89	9.9	14.7	3.4
Long days (Summer)	May 7	Aug 5	91	14.8	16.0	1.6

Table 2.3. Seasonal changes in body mass, energy intake, and requirements of captive phocid seals. Means from each seal used in these calculations were previously weighted by the number of observations taken from each individual.

		Fall	Winter	Spring	Summer
<i>Pagophilus groenlandicus</i>					
Number of seals studied		7	7	7	8
Seasons per seal		3.2	3.2	3.4	3.7
Body mass, kg	Mean	133.6	159.2	163.8	131.7
	SE	29.44	31.05	21.91	22.17
Daily mass change, g/d	Mean	53.5	440.9	-326.5	-39.2
	SE	104.31	71.84	281.11	142.16
Maintenance energy, MJ/d	Mean	24.3	34.7	38.7	27.1
	SE	1.41	2.49	4.96	1.84
Digestible energy, MJ/d	Mean	27.0	44.2	31.1	27.4
	SE	2.61	2.72	2.70	4.09
Growth efficiency, g/MJ	Mean	38.4	62.8	60.0	28.5
	SE	5.64	35.91	14.31	8.06
<i>Phoca vitulina</i>					
Number of seals studied		6	6	6	6
Seasons per seal		4.9	5.0	4.6	5.7
Body mass, kg	Mean	80.6	89.6	89.8	90.3
	SE	3.03	6.36	4.22	5.79
Daily mass change, g/d	Mean	132.6	48.5	44.3	-203.3
	SE	181.12	57.67	31.84	137.67
Maintenance energy, MJ/d	Mean	29.3	22.2	19.1	22.5
	SE	5.07	6.63	5.96	4.40
Digestible energy, MJ/d	Mean	31.3	25.2	22.9	21.4
	SE	2.67	4.31	4.31	2.87
Growth efficiency, g/MJ	Mean	94.5	4.3	205.2	13.1
	SE	138.00	49.96	490.82	42.83
<i>Phoca hispida</i>					
Number of seals studied		2	2	2	2
Seasons per seal		2.0	2.0	2.0	2.5
Body mass, kg	Mean	44.8	46.7	46.5	42.8
	SE	4.25	5.28	0.92	1.01
Daily mass change, g/d	Mean	16.4	0.6	29.8	-34.6
	SE	20.64	14.61	10.89	89.18
Maintenance energy, MJ/d	Mean	11.8	13.5	13.8	11.7
	SE	0.24			
Digestible energy, MJ/d	Mean	13.1	12.6	15.2	11.1
	SE	1.05	0.09	0.46	3.02
Growth efficiency, g/MJ	Mean	39.8	39.8	49.3	59.2
	SE	5.79			

Table 2.4. Yule-Walker probability values for the autocorrelation-corrected regression of daily energy intake (MJ/day) against date, daylength, temperature ($^{\circ}\text{C}$), and average solar radiation (MJ/m^2) for 16 northern phocid seals held captive at the Ocean Science Centre, Logy Bay, Newfoundland ($47^{\circ}38'\text{N}$, $52^{\circ}40'\text{W}$).

	Seal	Date	Daylength	Temperature	Solar Radiation
<i>Pagophilus groenlandicus</i>	BAB	0.0001	0.0001	0.0383	0.4354
	CHE	0.5836	0.9940	0.0789	0.9044
	ELM	0.0084	0.0002	0.5416	0.5857
	MIC	0.0001	0.0001	0.1954	0.0154
	RHO	0.0017	0.0001	0.0735	0.6748
	TYL	0.1280	0.0040	0.9822	0.6708
	VIC	0.6501	0.0134	0.8019	0.2063
	VIR	0.0002	0.0001	0.1746	0.3579
<i>Phoca vitulina</i>	CAE	0.0112	0.0051	0.0063	0.0728
	CLA	0.0087	0.0064	0.3327	0.4478
	DAR	0.2370	0.7146	0.2424	0.2767
	JUL	0.1130	0.0076	0.0046	0.3369
	KEV	0.3148	0.0230	0.3047	0.4187
	OSC	0.6162	0.0076	0.0778	0.6011
<i>P. hispida</i>	LER	0.1424	0.1524	0.6586	0.4824
	MEG	0.0205	0.0090	0.5848	0.3169

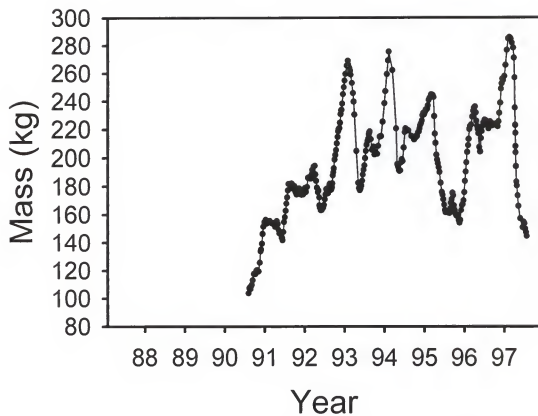


Figure 2.1. Body mass record of female harp seal (*Pagophilus groenlandicus*) BAB kept outdoors in Logy Bay, Newfoundland (47°38'N, 52°40'W).

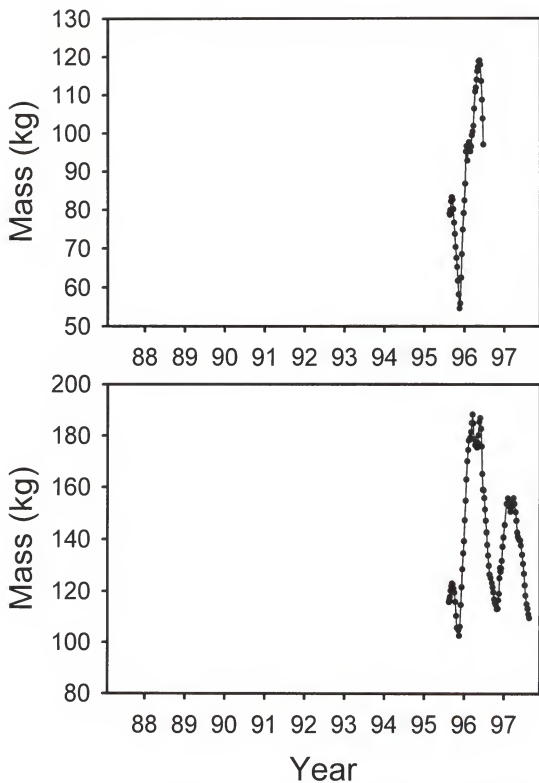


Figure 2.2. Body mass records of harp seals (*Pagophilus groenlandicus*) kept outdoors in Logy Bay, Newfoundland (47°38'N, 52°40'W). a) female CHE; b) male ELM.

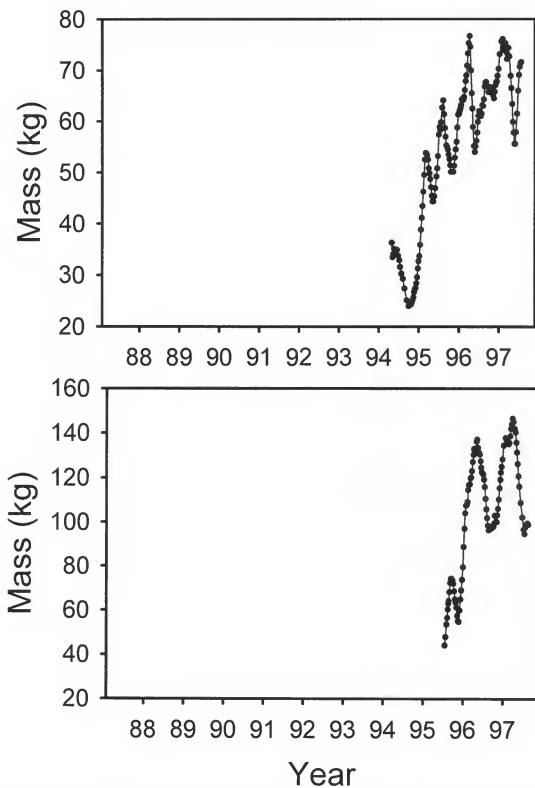


Figure 2.3. Body mass records of harp seals (*Pagophilus groenlandicus*) kept outdoors in Logy Bay, Newfoundland (47°38'N, 52°40'W). a) male JAM; b) male MIC.

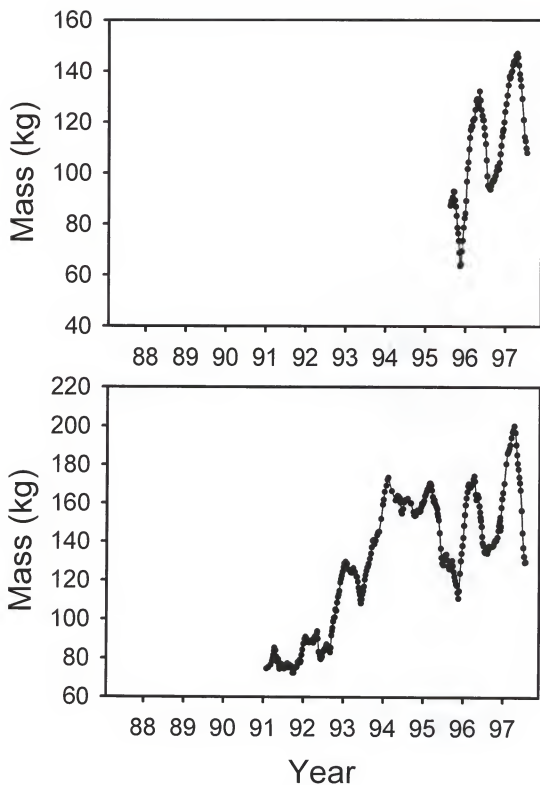


Figure 2.4. Body mass records of harp seals (*Pagophilus groenlandicus*) kept outdoors in Logy Bay, Newfoundland (47°38'N, 52°40'W). a) female RHO; b) male TYL.

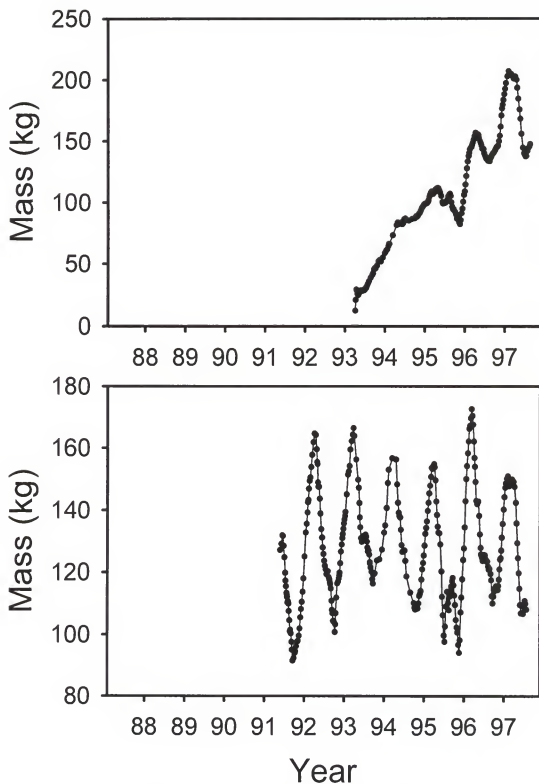


Figure 2.5. Body mass records of harp seals (*Pagophilus groenlandicus*) kept outdoors in Logy Bay, Newfoundland (47°38'N, 52°40'W). a) male VIC; b) male VIR.

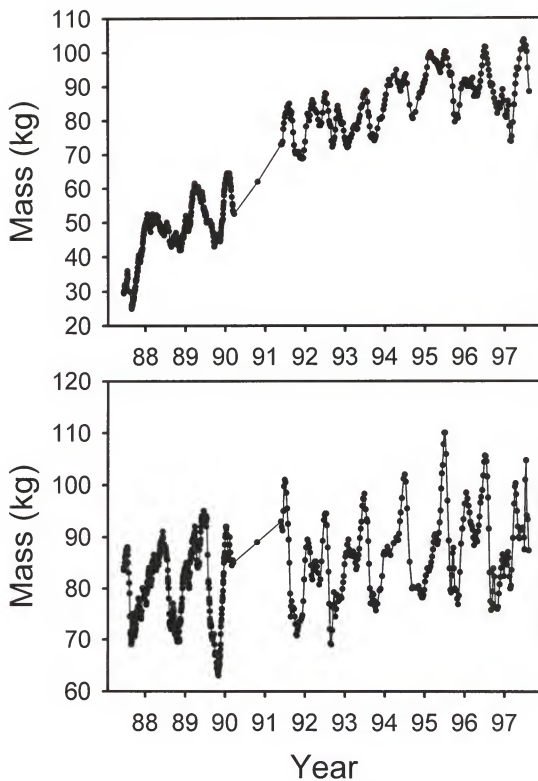


Figure 2.6. Body mass records of harbor seals (*Phoca vitulina*) kept outdoors in Logy Bay, Newfoundland (47°38'N, 52°40'W). a) male CAE; b) male CLA.

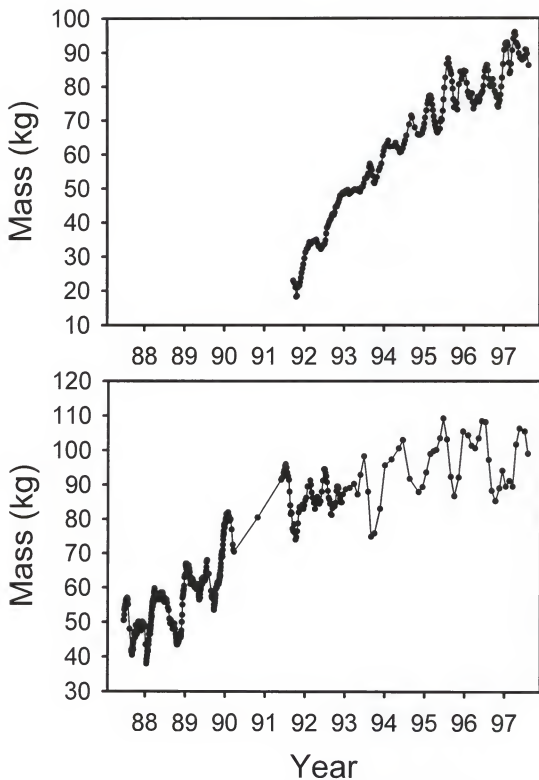


Figure 2.7. Body mass records of harbor seals (*Phoca vitulina*) kept outdoors in Logy Bay, Newfoundland (47°38'N, 52°40'W). a) male DAR; b) male JUL.

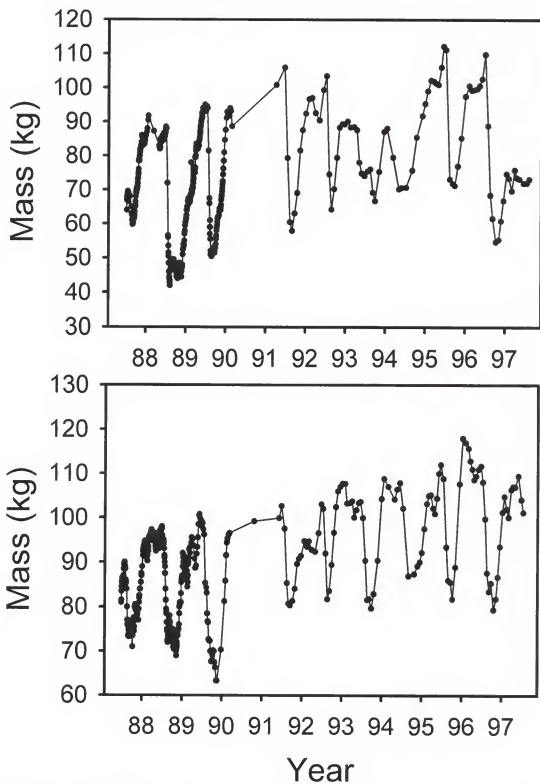


Figure 2.8. Body mass records of harbor seals (*Phoca vitulina*) kept outdoors in Logy Bay, Newfoundland (47°38'N, 52°40'W). a) female KEV; b) male OSC.

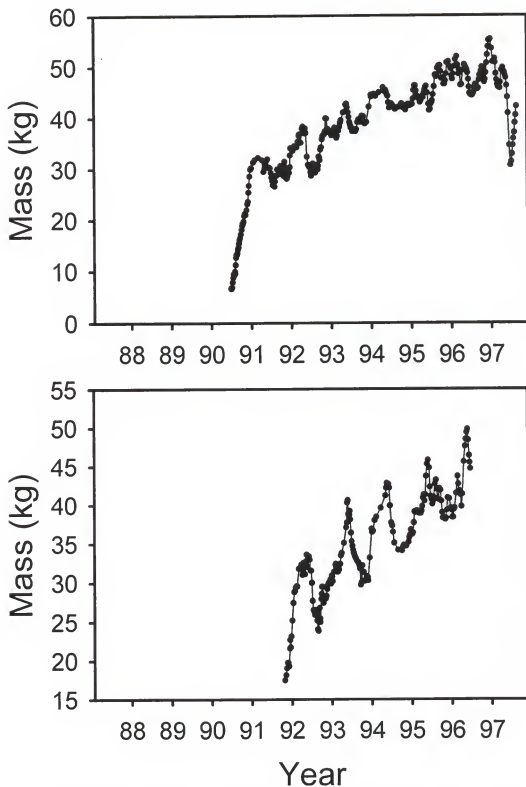


Figure 2.9. Body mass records of ringed seals (*Phoca hispida*) kept outdoors in Logy Bay, Newfoundland (47°38'N, 52°40'W). a) male LER; b) female MEG.

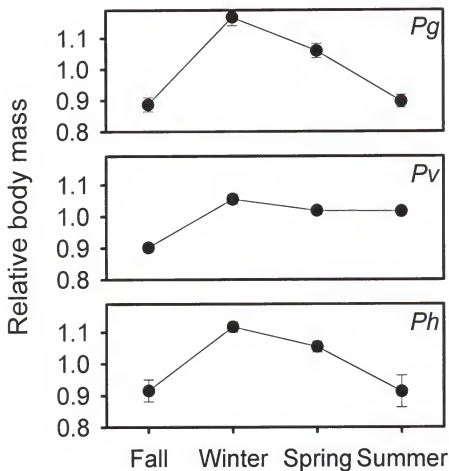


Figure 2.10. Seasonal changes in relative body mass (mass observed / mass predicted by the regression of mass against date) in seven adult harp seals (*Pagophilus groenlandicus*, *Pg*); six harbor seals (*Phoca vitulina*, *Pv*); and two ringed seals (*Phoca hispida*, *Ph*). Animals were fed *ad libitum* and held outdoors at the Ocean Sciences Centre, Logy Bay, Newfoundland (47°38'N, 52°40'W).

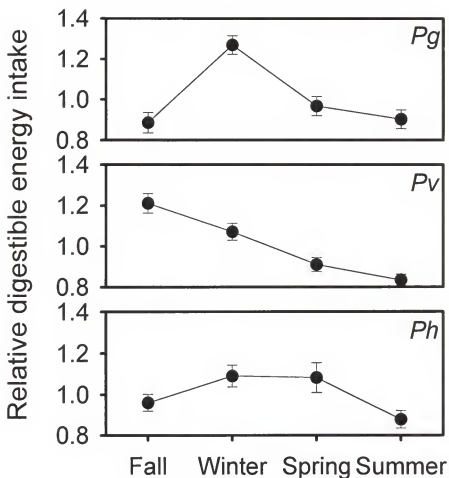


Figure 2.11. Seasonal changes in relative digestible energy intake, DEI (DEI observed / DEI predicted by the regression of DEI against date) in seven adult harp seals (*Pagophilus groenlandicus*, *Pg*); six harbor seals (*Phoca vitulina*, *Pv*); and two ringed seals (*Phoca hispida*, *Ph*). Animals were fed *ad libitum* and held outdoors at the Ocean Sciences Centre, Logy Bay, Newfoundland (47°38'N, 52°40'W).

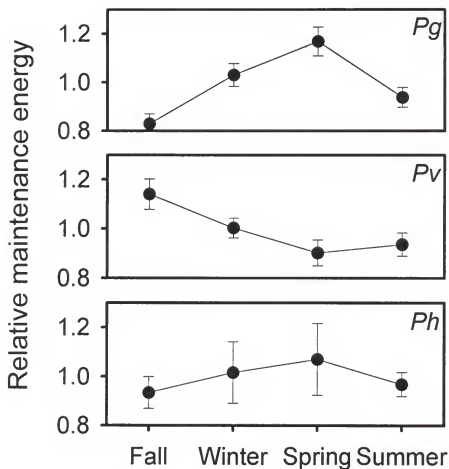


Figure 2.12. Seasonal changes in relative maintenance energy requirements, MER (MER observed / MER predicted by the regression of MER against date) in seven adult harp seals (*Pagophilus groenlandicus*, Pg); six harbor seals (*Phoca vitulina*, Pv); and two ringed seals (*Phoca hispida*, Ph). Animals were fed *ad libitum* and held outdoors at the Ocean Sciences Centre, Logy Bay, Newfoundland (47°38'N, 52°40'W).

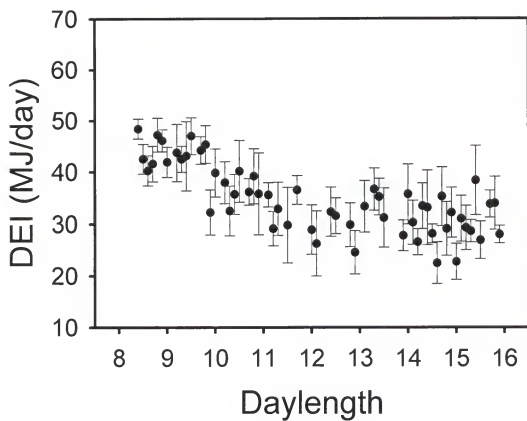


Figure 2.13. Relationship between photoperiod and food intake of adult harp seals (*Pagophilus groenlandicus*) kept outdoors at the Ocean Sciences Centre, Logy Bay, Newfoundland (47°38'N, 52°40'W).

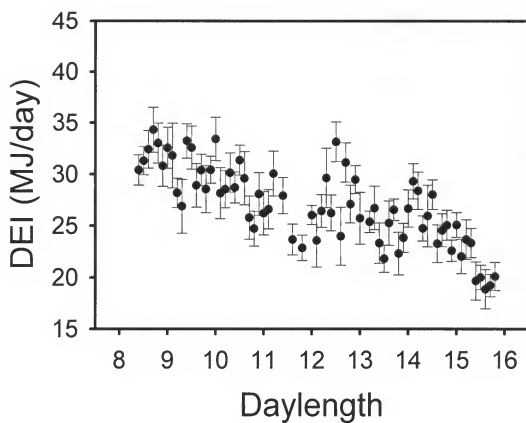


Figure 2.14. Relationship between photoperiod and food intake of adult harbor seals (*Phoca vitulina*) kept outdoors at the Ocean Sciences Centre, Logy Bay, Newfoundland (47°38'N, 52°40'W).

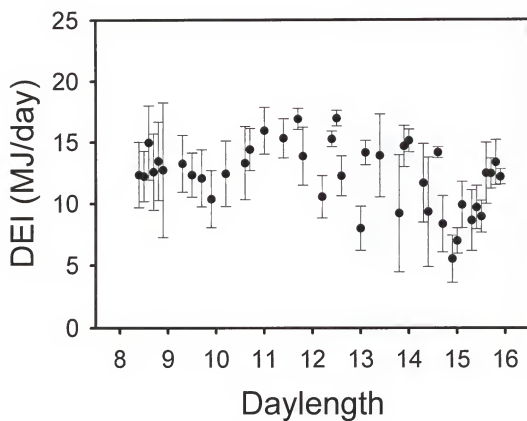


Figure 2.15. Relationship between photoperiod and food intake of adult ringed seals (*Phoca hispida*) kept outdoors at the Ocean Sciences Centre, Logy Bay, Newfoundland (47°38'N, 52°40'W).

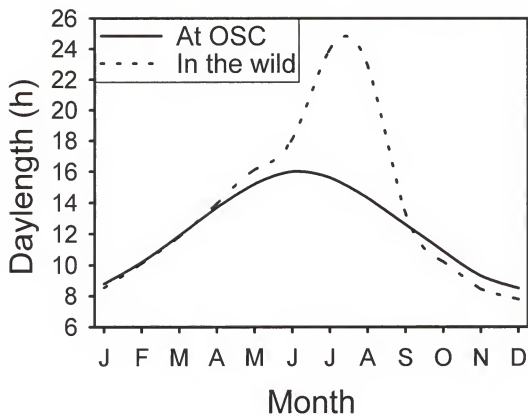


Figure 2.16. Photoperiods experienced by captive harp seals (*Pagophilus groenlandicus*) kept at the Ocean Sciences Centre (OSC), Logy Bay, Newfoundland (47°38'N, 52°40'W), and that hypothesized for harp seals in the wild during their annual migration.

CHAPTER 3 BASAL RATES OF METABOLISM OF PHOCID SEALS

Introduction

Pinnipeds are an especially difficult group within which study basal rates of metabolism. Their body sizes range from large to enormous (25 to 4,000 kg); live in both aquatic and the terrestrial environments; and are likely to undergo profound metabolic changes throughout the annual cycle, from intense feeding to fasting while reproducing and moulting. Major problems with the existing data on pinniped metabolic rates include the use of immature animals, the measurement of metabolic rates in restrained animals, and the lack of control for activity, post absorptive status, and period of inactivity (Schmitz and Lavigne 1984, Lavigne et al. 1986).

Growing mammals clearly exhibit increased metabolic rates in relation to their body size (Brody 1945). Restrained animals, on the other hand, can be under severe stress, exhibiting high metabolic rates. Conversely, it has been observed that metabolic rates are depressed during diving activity (Kooyman et al. 1980). In addition, oxygen consumption decreases during sleep. As an example, fasting grey seal pups can lower their metabolic rate as much as 48 % when sleeping (Worthy 1987). Also, in the California sea lion, metabolic rate while sleeping can be 24 % less than when

awake (Matsuura and Whittow 1973). It is clear that measurements of metabolic rates under standard conditions are needed to build meaningful energy budgets for pinnipeds.

My objectives were to determine basal rates of metabolism on three species of phocid seals. Concurrently, I also intended to establish the changes in metabolic rate due to age, to determine the possible differences in metabolic rates between seals in water and resting on a dry substrate, and to explore whether moulting had an effect on metabolic rates.

Material and Methods

I measured metabolic rates of nine harp, three harbor, and one ringed seal by determining their rate of oxygen consumption through open-flow respirometry. Oxygen consumption was measured from post-absorptive (> 16 h post-prandial) animals at different ambient temperatures for periods of two to four hours.

To measure oxygen consumption in air, I built a metabolic chamber to control ambient temperature during determinations. The chamber was 2.4 x 1.0 x 0.9 m internally, with an empty volume of 2.16 m³. It had two doors and a temperature-control system consisting of a water bath of 11,000 BTU capacity that controlled the temperature of a glycol solution pumped through a series of radiators inside the metabolic chamber to maintain a constant internal temperature (Figure 3.1). The measurement of oxygen consumption throughout a range of ambient temperatures gave certainty that metabolic measurements were made within the range

of thermal neutrality, a basic condition for obtaining valid estimates of basal metabolism.

For some animals, I measured oxygen consumption while the seal was in water, as well as when it was in air. For the former, I used a 1.8-m diameter tank filled with water just enough depth to keep the seal submersed to minimize the space available for swimming. This tank was airtight; it was also designed for measurements of oxygen consumption by other researchers (Renouf and Gales 1994). The tank was filled with non-circulating seawater pumped from the nearby Logy Bay. Water temperatures during measurements ranged between 0 and 3°C.

Fresh air was pumped to both chambers at a rate that varied between 100 and 150 l/min, depending on the size of the animal. The flow rate was measured using a Cole-Parmer gravimetric flowmeter (Vernon Hills, Illinois). Given the large volumes of air introduced in the chamber, no attempt was made to remove water before measuring the airflow. Consequently, the humidity of the incoming air was constantly measured using a Cole-Parmer thermohygrometer (Vernon Hills, Illinois) to subtract the volume of water vapor from the volume of air introduced in the chamber.

A small sample of air was constantly drawn from the chamber at a rate of 150 ml/min. This air sample was first passed through soda lime and silica gel to remove carbon dioxide and water, respectively. The content of oxygen in the sample of air was then determined using a SA-3 AMETEK oxygen analyzer (Pittsburgh, Pennsylvania). The temperature of the chambers, and that of the

air at the point of measurement of flowrate, was determined with copper-constantan thermocouples.

The calculation of the rate of oxygen consumption was made using the oxygen concentration that was maintained constant for at least 10 min during the two- to four-hour measurement period. Animals were first acclimatized to the chamber for periods of 2-4 hours during two weeks before commencing measurements.

I tested possible differences in resting metabolic rates between measurements done in water and in air and between measurements performed during the moult or before its onset using paired t-tests of data collected from the same animals during the same season. I tested for the effect of body mass and age on resting metabolic rates using correlation analysis. I also tested the hypothesis that basal rates of metabolism of northern seals are not different from those of terrestrial mammals by comparing them to those calculated using predictive equations available from the literature (Kleiber 1961).

Results

Rates of oxygen consumption of seals measured while resting varied between 14.2 and 39.6 l/min, whereas mass-specific rates ranged between 0.17 and 0.38 ml/g h (Table 3.1). The comparison of rates of oxygen consumption taken while the animal was in water and in air revealed no differences (paired t-test = -0.25, d.f. = 8, $P = 0.807$). However, the ring seal did increase its metabolic

rate while in water by 54%, probably because its small size allowed it to swim despite the small amount of water in the tank.

The moult did not have an effect on metabolic rates. The comparison of measurements of rates of oxygen consumption of seals during the moult period and before its onset revealed no significant differences (paired t -test = 1.4, d.f. = 7, P = 0.22).

Metabolic rates of adult harp seals did not change with ambient temperature in the range of -12 to 15°C. Above this temperature, there was an increase in the rate of oxygen consumption (Figure 3.2). Consequently, only values obtained below 15°C ambient temperature were used to estimate basal rates of metabolism.

I found that the adult seals had basal rates of metabolism higher than predicted by Kleiber's (1961) equation (paired t -test = 4.1, d.f. = 9, P < 0.003). Harp seals had a basal rates of metabolism 29 % higher than expected (paired t -test = 2.2, d.f. = 5, P < 0.04), whereas the basal rate of metabolism of harbor seals was 69 % higher than expected for mammals of similar size (paired t -test = 5.5, d.f. = 2, P < 0.02). The only ring seal studied had a basal rate of metabolism 45 % higher than expected for its mass.

Regression analyses demonstrated a significant logarithmic relationship between resting rates of metabolism and mass of the seals studied (r^2 = 0.72, d.f. = 11, P < 0.0003). Basal metabolic rates of adult seals were also related to body mass (r^2 = 0.48,

d.f. = 8, $P < 0.026$), and best described by the formula: $\dot{V}O_2$ (ml/g h) = $2.21 \cdot M_b(g)^{-0.55}$ (Figure 3.3).

Body temperature did not change with ambient temperature in two of the three adult male harp seals studied ($r^2 = 0.004$, d.f. = 27, $P = 0.74$), but increased with decreasing ambient temperatures in the male harp seal ELM ($r^2 = 0.53$, d.f. = 12, $P = 0.006$) (Figure 3.4).

Discussion

Metabolic rates measured while the animal was in water were not different from those measured while in air. However, when the animal was allowed to swim, metabolic rates were higher in water. Aside from the complications inherent to the difficulty of controlling activity in water, it has been found that metabolic rates are inversely correlated to the proportion of time spent underwater (harp seals, Gallivan 1981; Weddell seals, Castellini et al. 1992). Despite the fact that I did not find differences between measurements made in water or air, it is still preferable, for the sake of comparability, to use measurements of oxygen consumption in air to estimate basal rates of metabolism of pinnipeds.

There were no differences between metabolic rates before or during the moult in harp seals. There are conflicting reports regarding the influence of moult on phocid energetics. On one hand, some studies have documented a decrease in basal metabolic rates during the moult in yearling harbor seals (Ashwell-Erickson

and Elsner 1981). These authors suggested that the decrease might be due to the observed decrease in plasma thyroxine that has been reported during moult. However, other studies have produced conflicting results in relation to changes in the levels of thyroxine during moult. Harbor seals kept at the Ocean Sciences Centre showed no clear pattern of thyroxine levels in relation to the moult. Indeed, two animals had the highest thyroxine plasma level of a complete year cycle during the moulting period (Renouf and Brotea 1991). On the other hand, grey seals showed that juveniles had higher resting metabolic rates during the moult, but adults did not (Boily and Lavigne 1997). During the moult, phocid seals tend to spend more time hauled out and thus they probably have lower levels of activity and food intake. The increased time hauled out has been hypothesized to be due to the requirement for a higher skin temperature to promote rapid skin and hair regeneration (Ling 1974).

The thermoneutral zone, the range of ambient temperature in which the rate of metabolism is minimal and independent of temperature, ranged between 15°C and, at least, -12°C. Irving and Hart (1957) found that young harbor seals did not increase metabolic rates between -10 and 30°C while in air. The same animals increased metabolic rate when in water below 10°C. In contrast, Hansen *et al.* (1995) found that juvenile harbor seals increased their rate of metabolism below -2.3°C and above 25°C air temperature. Rates of metabolism for an adult harbor seal have been reported to stay constant from 20 to 35°C ambient

temperature, although an increase in rectal temperature was observed above 30°C ambient temperature (Matsuura and Whittow 1973). The larger size and more arctic distribution of harp seals may explain why they have a larger ability to withstand low ambient temperatures than harbor seals and start to increase metabolic rates when ambient temperature rises above only 15°C. Unlike harbor seals, harp seals always haul out on pack ice where ambient temperatures are low and windshield effects are likely to be important.

I found that basal rates of metabolism of the three species of phocid seal studied were higher than values predicted by Kleiber's (1961) equation. Another recent study of basal metabolism of grey seals found basal rates 10 to 50 % higher than those predicted by mass using Kleiber's (1961) relationship (Boily and Lavigne 1997). Higher metabolic rates of pinnipeds may not be related to aquatic habits, as was originally proposed (Schmidt-Nielsen 1983), but to their food habits. Terrestrial strict carnivore groups, such as felids, also have basal metabolic rates that are higher than predicted by mass (McNab, pers. comm.). The long-standing controversy regarding whether pinnipeds (and marine mammals in general) have higher basal rates of metabolism may have arisen from the lack of control of the variables that influence basal rates. Measurements taken at different times of the year can provide different estimates of basal rates (Boily and Lavigne 1997, chapter 4, this study). Also, the use of forced restraint, the lack of control of activity, and the allowance of diving might

contribute to the variation in reported values. Furthermore, the fact that basal rates of metabolism of a species do not differ from those predicted using Kleiber's (1961) equation does not mean that they are not different from those of terrestrial mammals. Kleiber based his equation on a limited set of species, mostly domesticated, and thus, it cannot be assumed that it will represent the "average" terrestrial mammal (McNab 1997).

Table 3.1. Total ($\dot{V}O_2$) and mass-specific ($\dot{V}O_2/M_b$) resting metabolic rates of individual harp *Pagophilus groenlandicus*, harbor *Phoca vitulina*, and ringed *P. hispida* seals.

Seal	N	Age (months)		Body mass (kg)	$\dot{V}O_2$ (l/h)	$\dot{V}O_2/M_b$ (ml/g h)
<i>Pagophilus groenlandicus</i>						
BAB	11	> 144	Mean	219.6	39.5	0.18
			SE	16.52	0.18	0.017
BRU	7	1	Mean	31.8	10.9	0.34
			SE	3.78	0.34	0.068
ELM	43	> 144	Mean	132.1	32.3	0.24
			SE	2.26	0.24	0.008
JAM	5	37	Mean	71.0	20.1	0.28
			SE	0.67	0.28	0.041
MIC	7	> 84	Mean	102.8	32.0	0.31
			SE	0.60	0.31	0.008
RHO	6	> 84	Mean	100.7	34.4	0.34
			SE	3.27	0.34	0.011
TYL	64	81	Mean	163.0	27.3	0.17
			SE	2.91	0.17	0.006
VIC	5	45	Mean	173.2	39.6	0.23
			SE	12.30	0.23	0.008
VIR	53	> 144	Mean	128.2	26.5	0.21
			SE	1.99	0.21	0.006
<i>Phoca vitulina</i>						
CAE	5	129	Mean	81.6	31.2	0.38
			SE	0.35	0.38	0.052
CLA	9	225	Mean	85.8	24.5	0.29
			SE	1.33	0.29	0.023
JUL	5	141	Mean	89.0	29.7	0.33
			SE	2.73	0.33	0.036
<i>Phoca hispida</i>						
LER	8	81	Mean	44.6	14.2	0.32
			SE	3.57	0.32	0.037

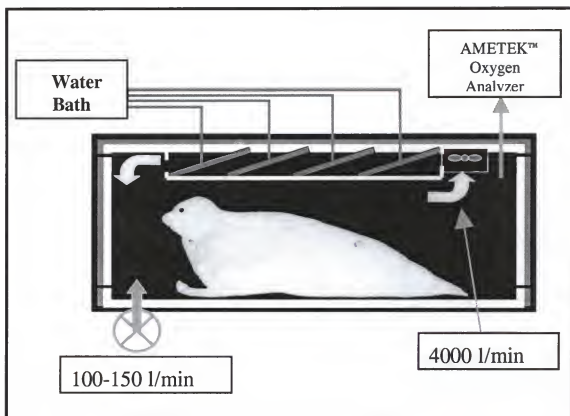


Figure 3.1. Metabolic chamber used in measuring oxygen consumption of phocid seals in air. A temperature-controlled water bath controlled the temperature of a glycol solution circulated through a series of four radiators placed in a special funnel inside the chamber. Air was forced through these radiators to control the chamber temperature.

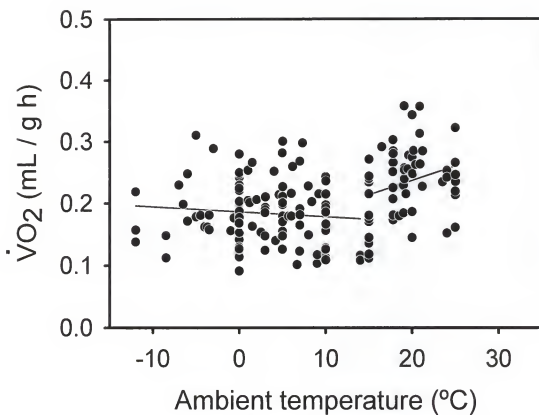


Figure 3.2. Relationship between resting oxygen consumption rate and ambient (air) temperature for three adult male harp seals (*Pagophilus groenlandicus*).

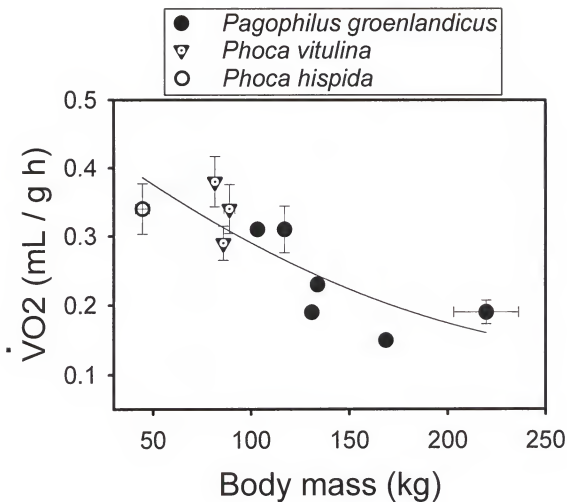


Figure 3.3. Oxygen consumption rates under basal conditions of six harp seals (*Pagophilus groenlandicus*), three harbor seals (*Phoca vitulina*), and one ring seal (*P. hispida*) in relation to their body mass.

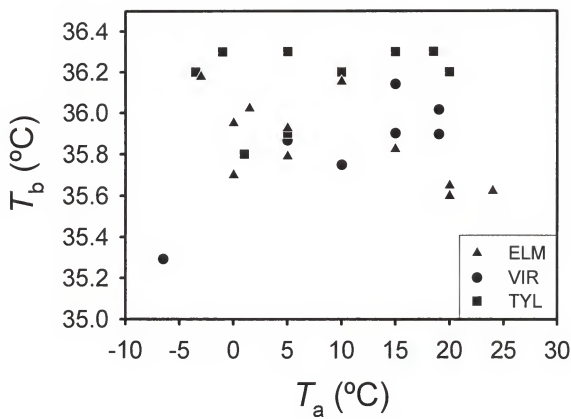


Figure 3.4. Body temperature of three adult male harp seals (*Pagophilus groenlandicus*) in relation to ambient (air) temperature.

CHAPTER 4
SEASONAL CHANGES IN BASAL RATES OF METABOLISM OF HARP SEALS

Introduction

A large proportion of the energy expenditure of endotherms is devoted to basal metabolism. Thus, animals might be expected to decrease these rates during periods when food is scarce or of poor quality. Basal rates of metabolism have been hypothesized to be merely the cost of maintaining the necessary metabolic machinery capable of producing maximum sustained metabolic rates, the ultimate target of natural selection (Kersten and Piersma 1987). A major contributor to basal rates of metabolism is respiration of organs involved in nutrient and energy processing, such as the alimentary tract, liver, and kidneys. In ruminants, it has been established that liver and gut are responsible for about 50 % of the basal metabolic expenditure (Johnson et al. 1990). A study comparing different strands of laboratory mice determined that basal metabolic rates were strongly correlated to the mass of internal organs (Konarzewski and Diamond 1995). In reproducing lab mice, principal component analysis demonstrated that the combined alimentary effects explained 72% of the variation in basal rates of metabolism (Speakman and McQueenie 1996).

The observed correlation between organ sizes and basal rates of metabolism may be interpreted as evidence for the ability to change basal rates in relation to the amount of nutrient and energy that needs to be processed. In this respect, basal rates were found to correlate with energy assimilation rates (*Falco tinnunculus*: Daan et al. 1989; lab mice: Konarzewski and Diamond 1994).

Given the profound variation in food intake and energy expenditure observed in pinnipeds in general, and phocid seals in particular (chapter 2) basal rates of metabolism may be hypothesized to vary throughout the annual cycle. Given that energy intake of harp seals, in relation to body mass, was shown minimal during summer and maximal during winter, I hypothesize that a similar trend will be observed for basal rates of metabolism. A previous study conducted at the Ocean Sciences Centre, however, concluded that harp seals had higher basal rates of metabolism during spring and summer as compared to the rest of the year (Renouf and Gales 1994).

Material and Methods

I measured metabolic rates of three adult male harp seals by determining their rate of oxygen consumption through open-flow respirometry. Oxygen consumption was measured from post-absorptive animals at different ambient temperatures for periods of 2-4 hours. Determinations of oxygen consumption rates were made in October, January, April, and July (10-18 per month). This design allowed me to compare basal rates of metabolism between

seasons with enough replicate measurements per seal to provide robust comparisons. I measured oxygen consumption following the methodology described in chapter 3. I tested the influence of seasonality using general linear models that included "seal" as a factor and body mass as a covariate.

Results

In total, I obtained more than 200 measurements of oxygen consumption rates throughout the entire study period. Metabolic rates of the three males studied were determined throughout a wide range of ambient temperatures (Figure 3.2). To estimate basal rates of metabolism, I chose to use only the measurements obtained below 15°C, given that seals increased their metabolic rate above this temperature ($t=2.1$, d.f. = 57, $P<0.04$). In this analysis, I used only 89 determinations of oxygen consumption that met the conditions for basal rates of metabolism.

Changes in basal metabolism and body mass throughout the annual cycle can be observed in Figures 4.1 - 4.3. I found that season had an effect on basal rates of metabolism. In the general model that included "seal" as a factor, season explained 32.9 % of the total variation in basal rates of metabolism ($F_{3,88} = 25.94$, $P < 0.0001$) and individual differences accounted for 33.5 % of that variation ($F_{2,88} = 26.39$, $P < 0.0001$). Body mass did not have an effect on basal rates of these three seals ($F_{1,88} = 0.26$, $P < 0.612$). Multiple comparisons revealed that the effect of season was due to summer values being lower than values from all other seasons. The analysis of data on a seal by seal basis showed the

same trend (Table 4.1). As in the overall test, basal rates during summer were lower than during the rest of the year for the three males studied (Table 4.2, Figures 4.1 - 4.3). The decline in basal metabolism during summer was remarkably similar among the three males studied. Summer basal rates were 60.4%, 59.3%, and 61.3% of the mean value for the rest of the year for the three adult males studied.

Mass-specific basal rates of metabolism were also influenced by seasonality. I found that 36.9% of the total variation in mass-specific rates was accounted by seasonal effects, while 32.8% was accounted by individual differences ($F_{3,88} = 33.63$, $P < 0.0001$; $F_{2,88} = 29.89$, $P < 0.0001$, respectively). Although body mass explained only 6.0% of the total variation in mass-specific basal rates of metabolism, it did have an effect ($F_{1,88} = 5.43$, $P < 0.0222$). Multiple comparisons demonstrated that only winter and summer values were not different. The analysis of the data from the individual seals produced similar results for the significance of the seasonal effects (Table 4.1), and the multiple seasonal comparisons (Table 4.2).

Discussion

My results support the hypothesis that basal rates of metabolism of phocid seals change throughout the annual cycle, and that this variation is probably related to the observed seasonal changes in food intake.

The confirmation of the expected trend of lower levels of basal metabolism during summer is at odds with previous research conducted by the late Dr. Renouf and collaborators on harp seals housed at the Ocean Sciences Centre. These researchers found that, contrary to predictions based on thermoregulatory and reproductive considerations, harp seals had higher basal rates of metabolism in summer than during the rest of the year. My results clearly contradict the previous report by Renouf and Gales (1994). At least two factors may explain this disagreement. First, the previous study measured oxygen consumption throughout a 24-hour cycle of seals kept in a tank fitted with a Plexiglas bubble from which air samples were drawn. Seals were free to swim inside the tank during that time. To control for the effect of physical activity on oxygen consumption, these authors chose the hour with the lowest oxygen consumption as a measure of basal rates. As such, the methodology was probably sensitive to seasonal changes in activity. The minimal activity in a 24-hour period of a male seal near the breeding season (especially if sexually mature females are nearby) might be higher than that of a resting seal. Another, perhaps more important drawback of the previous study is that the design was not balanced. Single 24-hour measurements were made at various intervals, from two weeks to two months. So, for some animals there were only two measurements representing an entire season.

In my design, I explicitly avoided the complications of allowing animals free movement during the determination of oxygen

consumption rate. As mentioned in the methods section of chapter 3, I used a "dry" metabolic chamber in which the animal laid down during measurements. In addition, I measured oxygen consumption rates of every seal more than 10 times each season, and kept the period between seasonal measurements constant (60 days).

I believe my results accurately reflect the changes in basal rates of metabolism experienced by harp seals in captivity, and in the wild. My results agree with what would be expected of mammals exposed to varying levels of food intake and energy balance. During spring and summer, although energy expenditure is relatively high, food consumption is not, resulting in a negative energy balance (body mass loss). As expected, basal rates are lower during this phase of the annual cycle, and probably represent an adaptation to slow the rate of body mass loss during this period. In addition, as food consumption is low, visceral organs probably recess in size and/or metabolic activity, as compared with periods of intense feeding during the fall.

A recent study has shown that captive grey seals have a similar pattern of seasonal changes in basal rates of metabolism. In that study, basal rates during the summer were found to be up to 50% lower than in the other seasons for the three females studied (Boily and Lavigne 1997). Unfortunately, these authors did not provide information on food intake levels or patterns of body mass change of these animals, although they stated the seals were fed and ate daily.

Table 4.1. Results of the analysis of variance, ANOVA (F statistic, F and probability value, P) used to test the influence of season on total ($\dot{V}O_2$) and mass-specific ($\dot{V}O_2/M_b$) basal metabolic rates of three adult male harp seals, *Pagophilus groenlandicus*.

Seal	$\dot{V}O_2$	$\dot{V}O_2$	$\dot{V}O_2/M_b$	$\dot{V}O_2/M_b$
	F	P	F	P
ELM	16.14	0.0001	11.91	0.0001
TYL	14.61	0.0001	21.98	0.0001
VIR	8.36	0.0002	6.89	0.0006

Table 4.2. Comparison of total ($\dot{V}O_2$) and mass-specific

($\dot{V}O_2/M_b$) basal metabolic rates among seasons for three adult harp seals, *Pagophilus groenlandicus*. Cells containing the "less than" sign (<) indicate that the first season represented in the column header had significantly lower values than the second season.

Variable	Seal	Su ¹ -W ²	Su-F ³	Su-Sp ⁴	W-F	Sp-F	W-Sp
$\dot{V}O_2$	ELM	<	<	<			
	TYL	<	<	<	<		
	VIR	<	<	<			
$\dot{V}O_2/M_b$	ELM		<	<	<		
	TYL		<	<	<	<	<
	VIR		<	<	<		<

¹ = summer, ² = winter, ³ = fall, ⁴ = spring

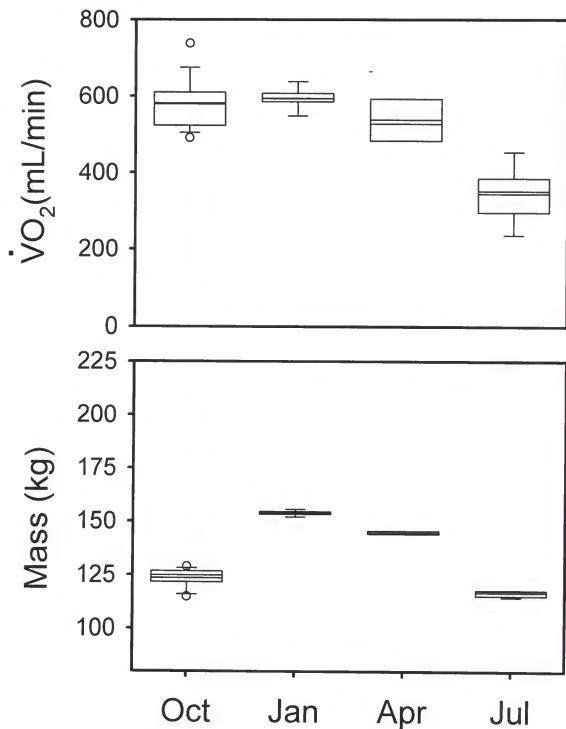


Figure 4.1. Seasonal variation in basal rates of oxygen consumption (top) and body mass (bottom) of the adult male harp seal, *Pagophilus groenlandicus*, ELM.

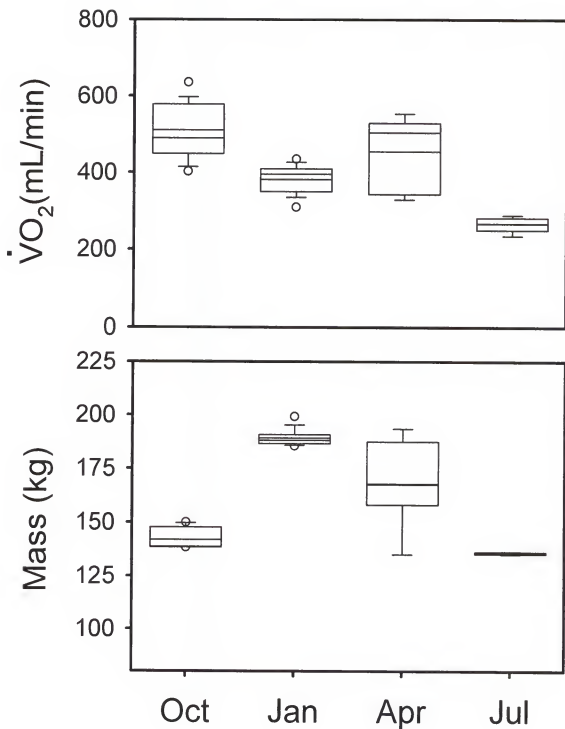


Figure 4.2. Seasonal variation in basal rates of oxygen consumption (top) and body mass (bottom) of the adult male harp seal, *Pagophilus groenlandicus*, TYL.

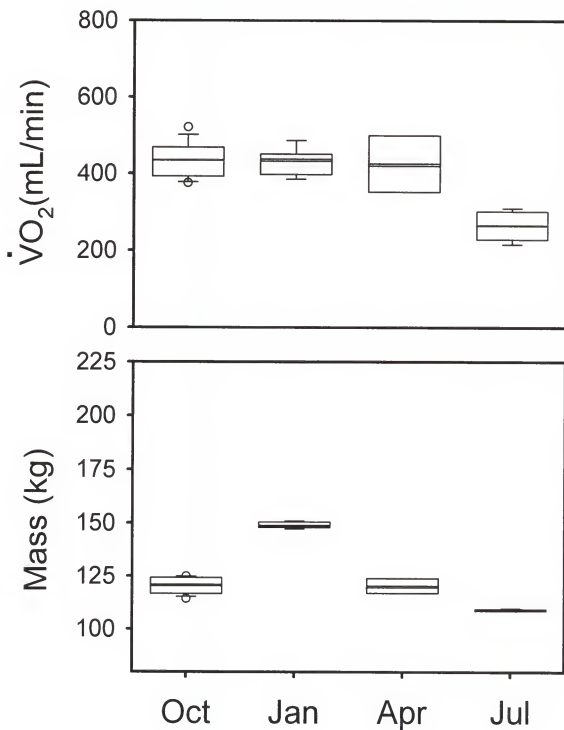


Figure 4.3. Seasonal variation in basal rates of oxygen consumption (top) and body mass (bottom) of the adult male harp seal, *Pagophilus groenlandicus*, VIR.

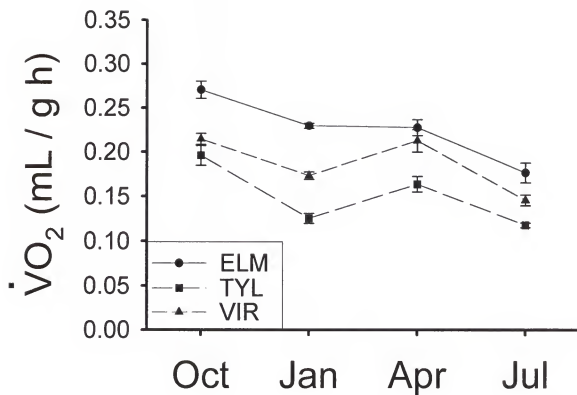


Figure 4.4. Seasonal variation in mass-specific basal rates of oxygen consumption for three adult male harp seals (*Pagophilus groenlandicus*).

CHAPTER 5
INFLUENCE OF BODY COMPOSITION ON SEASONAL CHANGES OF ENERGY
EXPENDITURE OF CAPTIVE HARP SEALS

Introduction

Knowledge of body composition is essential for studies of energy allocation. As is well known, the energy equivalencies of the different components of the body are quite different, from 0 for water to 38.9 kJ/g for fat. Although most of the energy mobilized involves fat depots, a large proportion might involve changes in the lean portion of the body. In fasting northern elephant seal pups the proportion of body fat did not change during the 2-3 month postweaning fast (Adams and Costa 1993). Although the different body components were used in the same proportion, protein catabolism accounted for only 4% of the energy (Pernia et al. 1980, Rea and Costa 1992).

Changes in the body composition of animals may also affect rates of metabolism. Metabolic rates of human subjects correlate better with lean body mass than with total body mass (Felig et al. 1983, Segal et al. 1989), suggesting that fat tissue does not contribute to the total metabolism. However, other studies involving rats (*Rattus norvegicus*) and sheep have found that fat does contribute to the overall metabolism (McCracken and McNiven 1983, McNiven 1984).

The objectives of this part of the study were to determine the body composition of adult harp seals, and how it changes during the year. These results were used to determine the relationship between seasonal changes in body mass and changes in the energy content of the body, and between changes in body composition and the seasonal variation in metabolic rates.

Material and Methods

I determined the body composition of the four adult harp seals (BAB, ELM, TYL, and VIR) during each season. I used the method of isotope dilution (reviewed by Speakman 1997) that provides accurate estimates of the water content of the body. In early November, February, May, and July, each animal was physically restrained, after intramuscular administration of Valium (5 mg/ml, Roche Laboratories) at an approximate dose of 1.5 mL/100 kg, to facilitate handling. A known amount of deuterium oxide (D_2O , 99.9% purity, Cambridge Isotope Laboratories, Andover, MA) was administered using a stomach tube, at an approximate dose of 0.5 g/kg. The complete delivery of the isotope was secured by flushing the syringe and stomach tube with small amounts of water and air.

Blood samples were drawn from the venous plexus of the hind flippers at approximately 5, 20, and 28 h after administration of the isotope. During this time, animals were fasted and kept on deck. Blood samples were allowed to clot, and the plasma was then obtained and kept frozen at $-70^{\circ}C$ until analysis.

Laboratory Analyses

Water was obtained from plasma samples by distillation, using the method proposed by Oftedal and Iverson (1987). I heated each sample in 10-mL distillation tubes and collected the water in a side arm tube immersed in a mixture of ethyl alcohol and dry ice. The concentration of deuterium oxide in the water samples was then determined through mass ratio spectrophotometry (Speakman 1997).

Calculations

Concentrations of D_2O in plasma were used to determine water pool size (P) of seals. After log transformation of the plasma concentrations of D_2O , I regressed them against time after administration of the isotope, to calculate D_2O concentration at time of administration (Figure 5.1). This approach prevents the overestimation of water pool size that occurs when using the actual concentration of D_2O obtained after an equilibration time of 3-4 hours (Oftedal and Iverson 1987, Speakman 1997). Then, I calculated water pool size using the formula:

$$\text{Water pool size (P}_0\text{)} = [\text{D}_2\text{O}] \text{ at time of administration (C}_0\text{)} \cdot \text{D}_2\text{O administered}$$

Water pool size (P) was used to estimate lean body mass (LBM) using a ratio of 0.703 (P:LBM) determined by carcass analysis of adult harp seals (Gales et al. 1994). Body fat was determined as the difference between body mass and lean body mass. Protein was also estimated using the data obtained from carcass

analysis. That study found that 25.7% of LBM of adult harp seals was protein (Gales et al. 1994). I estimated energy content of the body using the energy equivalencies of 38.91 kJ/g for fat and of 23.64 kJ/g for protein (Ofstedal et al. 1987b).

Results

On average, adult harp seals were 43.6 ± 2.26 % water, 37.9 ± 3.22 % fat, and 15.9 ± 0.83 % protein, and had an energy density of 18.5 ± 1.06 MJ/kg (Table 5.1). Although body fat increased with body mass ($F_{1,15} = 49.19$, $P < 0.0001$), the proportion of body fat did not change in relation to body mass ($F_{1,15} = 3.3$, $P < 0.0926$; Figure 5.2).

Although seasonal variations in body composition were apparent, they were not significant ($F_{3,14} = 3.08$, $P = 0.0901$), and the only significant factor was "seal" ($F_{3,14} = 10.73$, $P = 0.0035$). Changes in body mass were not only a product of changes in fat depots, but they were also related to large changes in lean body mass. Although minimal body mass occurred during winter, the lowest proportion of body fat was observed during spring (Figure 5.3). Although body mass decreased more or less linearly from winter to summer, lean mass changed little from winter to spring, but changed rapidly from spring to summer. This was also reflected in that the average energetic density of body tissues increased from spring to summer (Figure 5.4).

Discussion

The four adult harp seals had different body compositions. The female BAB, and the male TYL had large fat depots for most of the study period, with a maximum of 63 and 46.7% body fat, respectively. However, body composition of these captive seals was comparable to that of wild seals studied through dissection and carcass analysis (Gales et al. 1994). In the present study body fat during spring averaged 31%, while it averaged 33.2% in the wild adult seals studied during the same season (Gales et al. 1994).

The method of isotope dilution has been proven to produce accurate estimations of body composition. Comparisons of total body water content with results from proximate composition analyses of carcasses, have shown that the differences between the two approaches is less than 2% (Lydersen et al. 1992, Oftedal et al. 1993).

This study is the first to show that the seasonal variation in body mass of harp seals is not solely the result of changes in the size of fat depots throughout the year. Given that mass changes have a different make-up during the different seasons, the same levels of body mass changes will imply different rates of energy deposition or mobilization.

Table 5.1. Body composition of adult harp seals throughout the year cycle. The amount of each of the different components is given in absolute (kg) and relative terms (percentage, in parentheses).

Seal	Season	Body mass (kg)	Lean body mass	Water	Fat	Protein	Other	Energy Density (MJ/kg)
ELM	Fall	127.4	91.8 (72.1)	64.6 (50.7)	35.6 (27.9)	23.6 (18.5)	3.7 (2.9)	15.2
	Winter	150.2	97.3 (64.8)	68.4 (45.5)	52.9 (35.2)	25.0 (16.6)	3.9 (2.6)	17.6
	Spring	139.0	100.3 (72.1)	70.5 (50.7)	38.7 (27.9)	25.8 (18.5)	4.0 (2.9)	15.2
	Summer	112.6	78.4 (69.6)	55.1 (48.9)	34.2 (30.4)	20.1 (17.9)	3.1 (2.8)	16.1
TYL	Fall	153.2	81.7 (53.3)	57.4 (37.5)	71.5 (46.7)	21.0 (13.7)	3.3 (2.1)	21.4
	Winter	188.8	101.9 (54.0)	71.6 (37.9)	86.9 (46.0)	26.2 (13.9)	4.1 (2.2)	21.2
	Spring	169.6	103.6 (61.1)	72.8 (42.9)	66.0 (38.9)	26.6 (15.7)	4.1 (2.4)	18.9
	Summer	133.1	70.9 (53.3)	49.9 (37.5)	62.2 (46.7)	18.2 (13.7)	2.8 (2.1)	21.4
VIR	Fall	124.4	72.5 (58.3)	51.0 (41.0)	51.9 (41.7)	18.6 (15.0)	2.9 (2.3)	19.8
	Winter	149.0	116.8 (78.4)	82.1 (55.1)	32.2 (21.6)	30.0 (20.1)	4.7 (3.1)	13.2
	Spring	106.4	91.4 (85.9)	64.2 (60.4)	15.0 (14.1)	23.5 (22.1)	3.7 (3.4)	10.7
	Summer	107.5	70.2 (65.3)	49.4 (45.9)	37.3 (34.7)	18.0 (16.8)	2.8 (2.6)	17.5
BAB	Winter	285.8	139.0 (48.7)	97.8 (34.2)	146.8 (51.3)	35.7 (12.5)	5.6 (1.9)	22.9
	Spring	149.4	85.3 (57.1)	60.0 (40.2)	64.1 (42.9)	21.9 (14.7)	3.4 (2.3)	20.2
	Summer	139.2	51.5 (37.0)	36.2 (26.0)	87.7 (63.0)	13.2 (9.5)	2.1 (1.5)	26.8

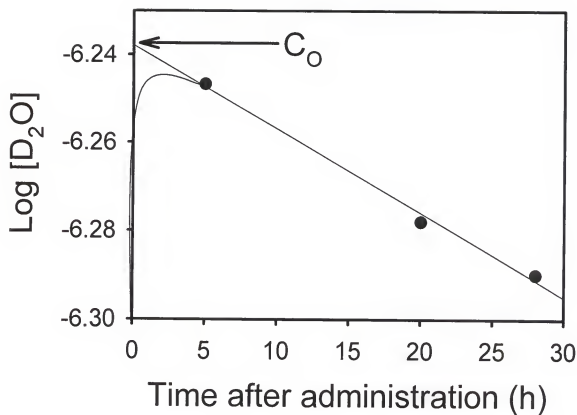


Figure 5.1. Methodology used to estimate concentration of deuterium oxide at time of administration (C_0). This method avoids the overestimation of total body water that occurs when the concentration determined from the first blood sample is used as an estimation of C_0 .

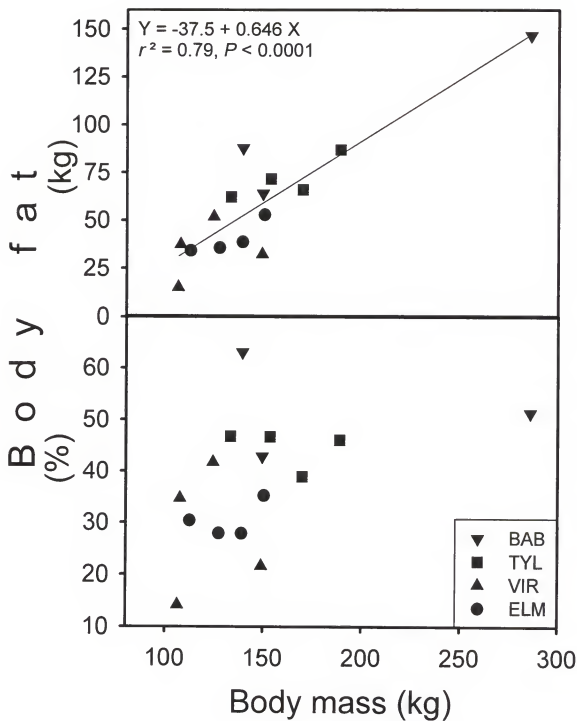


Figure 5.2. Relationship between body mass and absolute amount of body fat (top graph), and proportion of body fat (bottom graph) of four captive adult harp seals (*Pagophilus groenlandicus*).

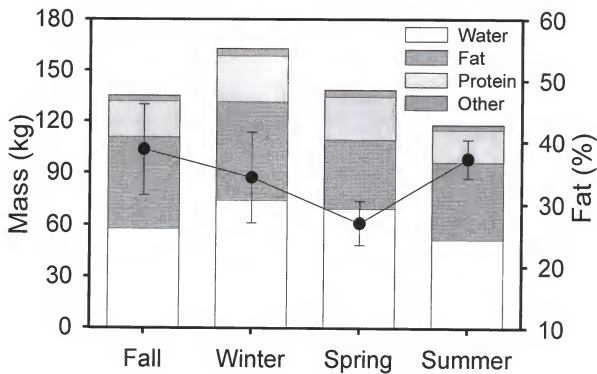


Figure 5.3. Seasonal changes in the components of the body and proportion of body fat of captive adult harp seals (*Pagophilus groenlandicus*).

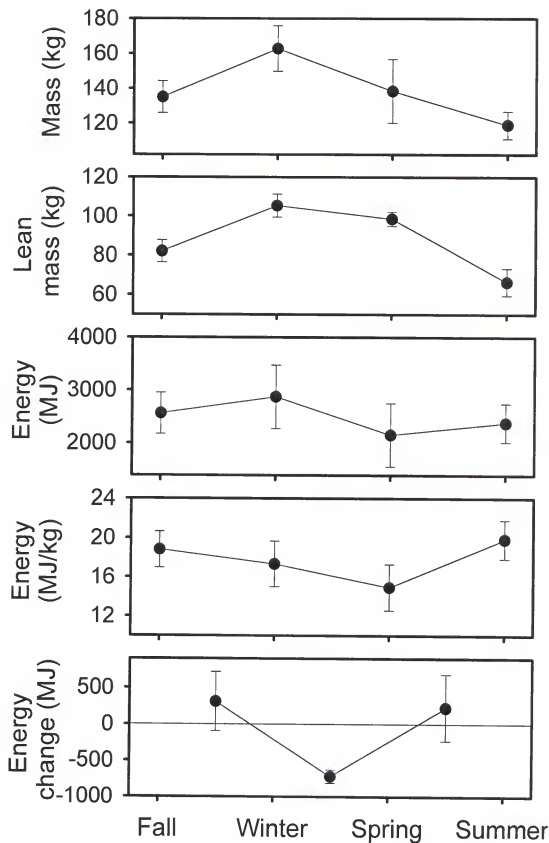


Figure 5.4. Seasonal changes in body composition and energy content of captive adult harp seals (*Pagophilus groenlandicus*).

CHAPTER 6 ACTIVITY LEVELS AND ENERGETIC COST OF ACTIVITY IN HARP SEALS

Introduction

Activity is an important component of the energy budget of animals. Locomotion in pinnipeds is aided by adaptations that reduce drag such as a streamlined body shape, and the power output needed for forward motion. Although the metabolic rate of terrestrial mammals increases linearly with speed, a curvilinear increase has been observed in seals. This increase in metabolic rate correlates with the curvilinear increase in drag as a function of speed (Williams and Kooyman 1985). Despite the effect of drag, pinnipeds use less energy for locomotion than terrestrial mammals of similar size, due in part to the absence of postural costs (Schmidt-Nielsen 1972, Feldkamp 1987).

Phocid seals propel themselves by alternate lateral sweeps of the hind flippers in a sculling action in conjunction with oscillations of the body (Tarasoff *et al.* 1972, Fish *et al.* 1988). The amplitude of the stroke does not change with swimming speed, and thus speed is linearly related to stroke frequency (Davis *et al.* 1985, Fish *et al.* 1988)

My objectives were to estimate the influence of activity on energy expenditure and food intake of harp seals, and to explore the influence of activity levels on the observed seasonal changes

of energy expenditure and food intake. This study was conducted in collaboration with Valerie Moulton, Master's student at the Biology Department, Memorial University of Newfoundland. She focused her study on the influence of weather and social interactions on activity levels of captive harp seals.

Material and Methods

Activity levels of harp seals were measured with simplified Mk6 time-depth recorders (Wildlife Computers, Redmond, Washington). These recorders detected changes of more than 45° in their position with respect to the horizontal and vertical planes. In addition, the recorders were fitted with conductivity pins that detected if the animal was in or out of the water. Data collected every minute on the minute was number of tilts ($> 45^\circ$) and dry or wet state.

The deployment of the activity recorders along the dorsal line between the second and third thirds of the body (Figure 6.1) allowed detection of hind flipper strokes used by phocid seals for propulsion. Although stroke frequency provides a measure of the speed of a particular seal, it does not provide a direct assessment of the energy expended in locomotion because metabolic rate increases exponentially with swimming speed (Williams and Kooyman 1985). Oxygen consumption of harbor seals swimming in an aquatic flume was proportional to swimming speed raised to the 1.42 power (Davis et al. 1985). To use tilt frequency measured by the activity recorder as an estimation of the energy spent in locomotion, I raised tilts per minute to the 1.42 power before

including this factor in the multivariate linear models used to detect the influence of activity on energy budgets.

I used the hourly average of tilt frequency for each of the animals for the analysis of circadian rhythms. I calculated average tilt frequency and time spent on deck (out of the water) for each of the periods between consecutive weightings to explore the relationship between activity and energy budgets. In addition, I calculated daily mass change (DMC, g/d) as the difference between two consecutive weighings, divided by the days elapsed between them. Daily food intake during each of the periods between consecutive weighings was averaged and multiplied by the energetic content of herring, and by its digestive efficiency (Lawson *et al.* 1997) (Table 2.1) to estimate digestible energy intake, DEI. To determine if activity changed throughout the year in a significant manner, I conducted ANOVAs using "season" and "seal" as factors.

Results

Circadian rhythms were apparent for the activity levels of harp seals. Levels of activity changed through the day in a consistent manner for all the seals studied (Figure 6.2). Activity tended to increase around midday, when the seals were fed. To determine if this circadian pattern had some relation with daylength, I regressed the coefficient of variation calculated for each day using mean of tilts per hour against photoperiod. The pattern of circadian variation in activity did

not change in relation to photoperiod. There was no clear pattern of changes in activity level among seasons (Figure 6.3).

I used multivariate linear models and regression analyses to determine if activity level, as measured by the activity data recorders, had a significant effect on the energy budget of captive harp seals. I first tested for the effect of the factors "seal" and "season" on daily mass change with a model that also included energy intake, body mass, proportion of time spent on deck (out of the water), and mean number of tilts raised to the 1.42 power (see Methods). The factors "seal" and "season", and the regressor body mass had no effect on the rate of mass change ($F_{8,258} = 1.74$, $P = 0.09$; $F_{3,258} = 2.61$, $P = 0.0522$; $F_{1,258} = 3.16$, $P = 0.077$, respectively). The proportion of time spent on deck explained 2.4% of the total variation on daily mass change and had an effect on the energy budget ($F_{1,258} = 4.61$, $P = 0.0328$). Energy intake explained 34.6% of the observed variation in daily mass change ($F_{1,258} = 67.21$, $P < 0.0001$). Activity level, measured as mean number of tilts raised to the 1.42 power, explained 3.2 % of the total variation observed in daily mass change ($F_{1,258} = 6.25$, $P < 0.0131$). The relationship between activity and daily mass change is presented in Figure 6.4, by plotting the residuals of the linear model of daily mass change against all the factors mentioned above except tilts per minute, against tilts per minute.

Discussion

The use of activity recorders provides information on the general level of activity of seals. However, the present

configuration of the system has major drawbacks. A major logistical limitation is that the sensor cannot be deployed too caudal on the animal's back to avoid its removal by the animal with its mouth. A more posterior deployment would ensure that the signal more accurately reflects the strokes used for propulsion by phocid seals. Another limitation of the system is that it cannot discern between tilts performed along the different axes. For the use of this device to estimate stroke frequency, it would be advantageous to limit the recording only to tilts performed in relation to the vertical axis. The fact that this was one of the first trials of this new technology precludes me to discuss my results with those of other investigators.

The measurement of stroke frequency can be used as an estimator on swimming speed because they are related linearly in phocid seals. An analysis of the data for three species provided in published reports (Davis *et al.* 1985, Fish *et al.* 1988) shows that swimming speed increases linearly with stroke frequency (Figure 6.5)

Although locomotion can be energetically expensive, its impact on the energy budget is generally low. It has been estimated that locomotor energy expenditure in terrestrial mammals requires less than 2% of the total field metabolic rate, and that this value is more or less independent of body mass (Altmann 1987). The fact that aquatic locomotion is less energetically expensive than terrestrial locomotion (Schmidt-Nielsen 1972, Feldkamp 1987) allows the inference that locomotion in phocid

seals also constitutes a small fraction of the overall energy budget.

The observation that the circadian rhythm of activity did not change with length of day points to the possibility that the increase in activity at midday was not related to the day/night phase, but was an artifact introduced by the maintenance activities performed by the seals' keepers. These activities included cleaning of decks and tanks, removing ice, and feeding the animals for two hours. A concurrent study demonstrated that seals spent less time resting on deck when disturbed, thus increasing time spent swimming (Moulton *et al.* In Press).

Differences in energy expenditure of harp seals between seasons were not due to differences in the levels of activity. Activity changed between seasons with no common pattern among the seals studied, whereas energy expenditure did (chapter 2).

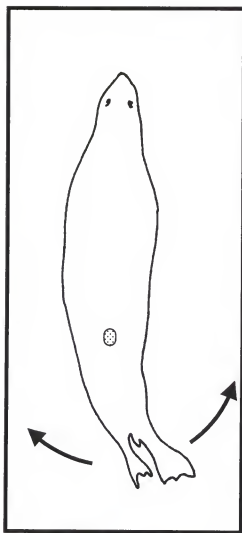


Figure 6.1. Diagram of a phocid seal swimming. These animals use lateral alternating movements of their hind flippers and posterior part of the body to produce thrust. The location of the activity recorder used to detect lateral strokes is marked by the shaded circle.

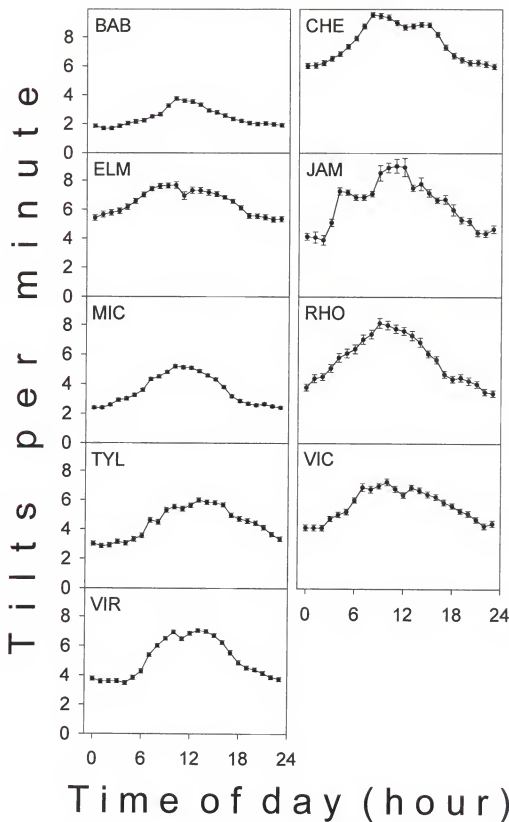


Figure 6.2. Activity levels of nine harp seals, *Pagophilus groenlandicus*, measured as tilts per minute in relation to time of day.

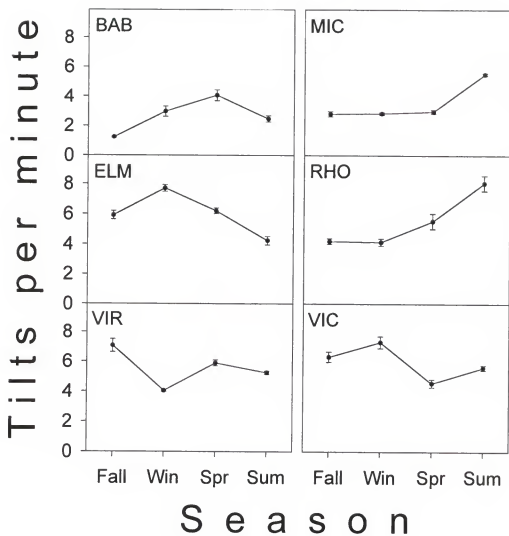


Figure 6.3. Changes in activity levels of captive harp seals, *Pagophilus groenlandicus*, measured as tilts per minute in relation to season.

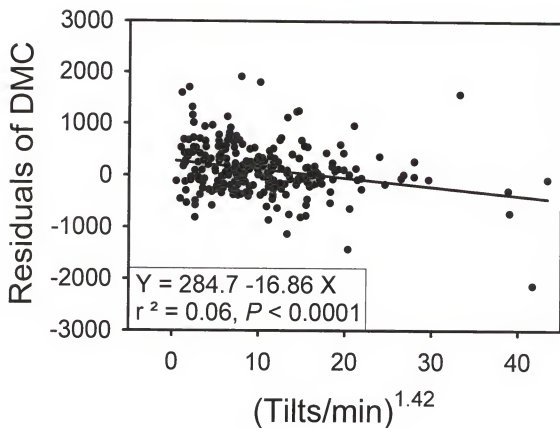


Figure 6.4. Influence of activity on daily mass change of captive harp seals, *Pagophilus groenlandicus*. The plot represents the relationship between an estimator of energy spent in locomotion [(tilts/min)^{1.42}] and the residuals of the linear model relating daily mass change (DMC,g) and the variables seal, season, mass (g), energy intake (kJ/day), and time spent on deck (%).

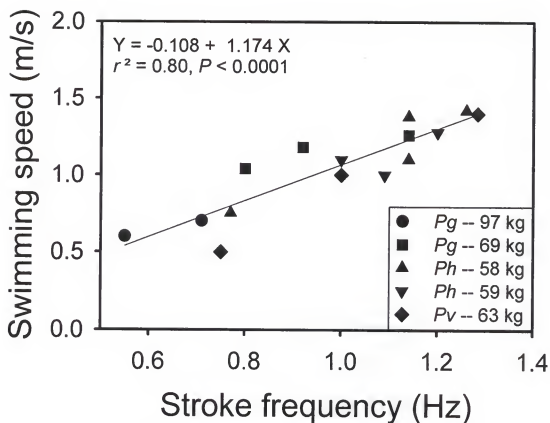


Figure 6.5. Relationship between the frequency of lateral strokes of the posterior part of the body and hind flippers, and swimming speed of phocid seals. Data from harp seals (*Pagophilus groenlandicus*, Pg) and ringed seals (*Phoca hispida*, Ph) from Fish et al. (1988); data from harbor seals (*Phoca vitulina*, Pv) from Davis et al. (1985).

CHAPTER 7 SYNTHESIS AND CONCLUSIONS

Basal Rates of Metabolism of Phocid Seals

A common criticism for using captive animals to estimate basal rates of metabolism is that husbandry conditions may reduce the opportunity for exercise, with the consequent decrease in muscle mass. This change may in turn reduce rates of metabolism given the high metabolic intensity of muscle. Despite the large variation in activity levels observed among the harp seals studied, I found no relationship between the level of activity and the measured basal rates of metabolism (Figure 7.1). Exercise may be a factor influencing basal rates of metabolism only when activity is severely limited. In this study, seals were free to swim in two 12-m diameter tanks or haul out on deck.

My results confirmed the view that phocid seals have basal rates of metabolism that are similar to those of other flesh-eating eutherians and, as such, they are higher than expected from Kleiber's (1961) relation, and by the relation calculated from McNab (1988) based on 321 wild mammal species. My data agree generally with information on basal rates obtained from several phocid seal species (Figure 7.2). The only exception is data from the ringed seal. Parsons (1977) studied four adult ringed seals and estimated basal rates well below the estimations using

Kleiber's (1961) relationship. In that study, energy intake was only 70% of the intake observed in my study for two adult ringed seals, suggesting that the low estimates of basal rates were not caused by methodological biases on the measurement of oxygen consumption. However, oxygen consumption rates were measured during only six 1-hour periods for each of the seals. In Parsons' (1977) study, all four seals were kept together in two tanks of 2.1 x 3.0 x 1.8 m. The limited space may have had severely constrained the ability of the animals to exercise, thus promoting a decrease in metabolic rate.

What Causes the Seasonal Changes in Energy Expenditure of Captive Harp Seals?

Harp, harbor, and ringed seals have profound seasonal changes in body mass and food intake, and that levels of energy expenditure of harp and harbor seals also changed throughout the annual cycle. The observation that these changes occur in animals fed ad libitum suggest they are controlled by some internal mechanism, probably triggered by some environmental cue, such as photoperiod.

Energy expenditure also varied throughout the annual cycle. The determination of basal rates of metabolism, and the energetic content of the body permits exploring the contribution of the various components of the energy budget to the observed seasonal variation in energy intake rates of captive harp seals. Basal metabolism was the largest component of the energy budget, comprising on average 45.5 % of the total energy expenditure

(Figure 7.3). Other expenditures (activity, some thermoregulatory costs) represented 35.9 % of the energy budget, whereas the deposition of body mass or mobilization of stores represented 2.4 %. The specific dynamic action of food (calculated as 17 % of the gross energy intake, Gallivan and Ronald 1981) accounted for 16.2 % of the total energy budget. Variations in basal metabolism represented 19.3 % of the seasonal variation in energy expenditure, whereas variations in other expenditures, and on changes in body stores, were responsible of 29.8 % and 40.0 %.

Implications for Modeling Energy Consumption in Wild Populations of Pinnipeds.

My results show the importance of incorporating temporal patterns into models that attempt to estimate fish consumption by populations of wild pinnipeds. This is especially important for migratory species that occupy sensitive areas only during some parts of the year, such as the harp seal. Captive adult harp seals consume, on average, 1.6 kg of fish per day. However, seals varied their level of fish consumption from 1.14 kg / day during summer, to 2.43 kg / day during winter. If we assume a population of 4 million harp seals for the northwest Atlantic, this difference will represent more than 1.87 million metric tons of fish per year. If a model maintains per capita consumption constant, it would have to assume that the population more than doubles from summer to winter, to accurately reflect the temporal distribution of fish consumption by the harp seal herd.

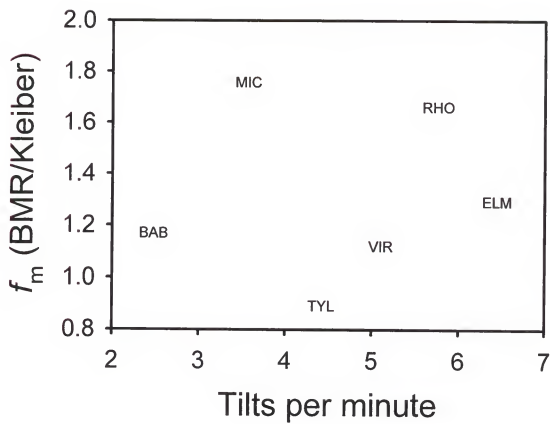


Figure 7.1. Basal rates of metabolism (relative to values predicted by body mass using Kleiber's 1961 relationship) and levels of activity measured as tilts per minute.

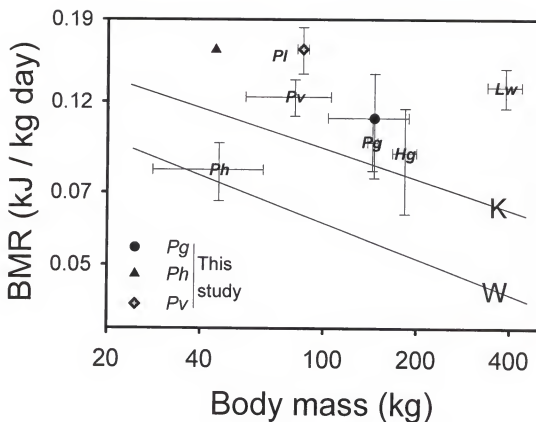


Figure 7.2. Basal rates of metabolism of several species of phocid seals obtained from this study and from published reports. *Halichoerus grypus*, Hg (Fedak and Anderson 1982, Boily and Lavigne 1995); *Leptonychotes weddellii*, Lw (Kooyman et al. 1973, Castellini et al. 1992); *Phoca hispida*, Ph (Parsons 1977); *P. largha*, Pl (Ashwell-Erickson and Elsner 1981); *P. vitulina*, Pv (Matsuura and Whittow 1973, Davis et al. 1985); *Pagophilus groenlandicus*, Pg (Gallivan and Ronald 1979, Renouf and Gales 1994). K represents the relationship calculated from Kleiber (1961), W represents the relationship calculated from McNab (1988).

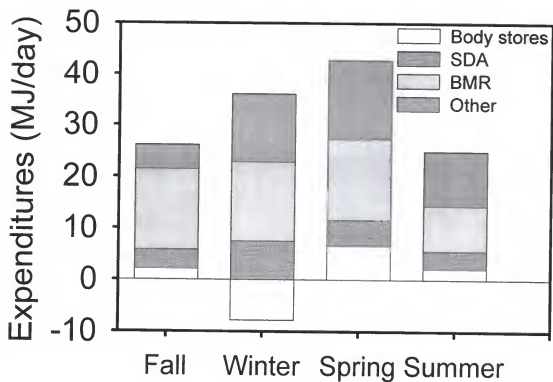


Figure 7.3. Changes in components of the energy budget of captive harp seals (*Pagophilus groenlandicus*) throughout the annual cycle.

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BIOGRAPHICAL SKETCH

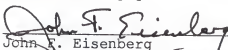
Hugo Ochoa-Acuña was born in Purranque, Chile, on September 18, 1962. He lived in Santiago, Chile, until 1975, when he moved to Buenos Aires, Argentina, where he attended High School. In 1981 Hugo entered the University of Chile in Santiago. He was awarded a Bachelor of Science degree in veterinary sciences in 1986 and a title in veterinary medicine in 1989. In 1987 he began a program of study on the ecology of the Juan Fernández fur seal with the guidance of Drs. John Francis and Daryl Boness from the National Zoological Park in Washington, D.C. In 1992 Hugo began graduate studies in the department of Wildlife Ecology and Conservation at the University of Florida where he obtained his master's degree in 1995, and his Ph.D. in Zoology in 1999.

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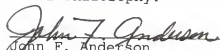
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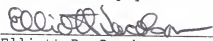
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John F. Anderson
Associate Professor of Zoology

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Elliott R. Jacobson
Professor of Veterinary
Medicine

This thesis was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August 1999

Dean, Graduate School